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*Festuca campestris* Rydb. Response to Fire and Defoliation

By

Amanda Dawn Bogen



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Master of Science*

in

Rangeland and Wildlife Resources

Department of Agricultural, Food and Nutritional Science

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled ***Festuca campestris Rydb.*** **Response to Fire and Defoliation** submitted by Amanda D. Bogen in partial fulfillment of the requirements for the degree of Master of Science in Rangeland and Wildlife Resources.





*I dedicate this thesis to my parents, Don and Ellen Bogen, for their endless support and encouragement.*

*“...And if inspir’d ‘tis Nature’s pow’rs inspire;  
Her’s all the melting thrill, and her’s the kindling fire.”*

*-Robert Burns (1759-1796)*





## Abstract

Concern has been expressed over recovery of the commercially and ecologically important native grass species, *Festuca campestris* Rydb., following wildfire. Ungrazed plants burned by wildfire declined in plant and tiller phytomass, inflorescence production, and height in the first and second growing season ( $p < 0.05$ ). Tiller number increased with burning in the second growing season ( $p < 0.05$ ). July defoliation reduced inflorescence production in unburned plants, and long-term phytomass and tiller number of burned plants ( $p < 0.05$ ). Burning and May defoliation reduced etiolated growth one year after fire. Defoliation intensity had no effect on burned plants, but decreased unburned plant phytomass and height ( $p < 0.05$ ).

A laboratory study used to evaluate *Festuca campestris* response to heat injury demonstrated there is an interaction between temperature and exposure time that affects tiller vigor ( $p < 0.05$ ). A reduction in plant tiller numbers and phytomass supported the conclusion that 60°C exceeds a threshold for causing injury to *Festuca campestris*.





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## Table of Contents

<b>1</b>	<b>INTRODUCTION .....</b>	<b>1</b>
1.1	LITERATURE CITED .....	5
<b>2</b>	<b>LITERATURE REVIEW.....</b>	<b>7</b>
2.1	FESCUE GRASSLANDS .....	7
2.1.1	<i>Climate</i> .....	7
2.1.2	<i>Geomorphology and Soils</i> .....	8
2.1.3	<i>Fescue Prairie Types</i> .....	9
2.1.3.1	<i>Festuca campestris</i> Rydb. – <i>Danthonia parryii</i> Scribn. Range Type .....	10
2.1.3.2	<i>Festuca hallii</i> (Vassey) Piper – <i>Stipa curiseta</i> A.S. Hitchc. Range Type .....	11
2.1.4	<i>Ecology and Use</i> .....	12
2.2	ROUGH FESCUE .....	13
2.2.1	<i>Taxonomy</i> .....	13
2.2.2	<i>Grazing Effects on Rough Fescue</i> .....	15
2.2.2.1	Soil Changes.....	15
2.2.2.2	Fescue Grassland Vegetational Response to Grazing .....	16
2.2.2.3	Rough Fescue Plant Response to Grazing.....	18
2.2.3	<i>Fire Effects on Rough Fescue</i> .....	21
2.2.3.1	Microclimate Changes Following Fire.....	24
2.2.3.2	Cover and Production Changes with Fire .....	25
2.2.3.3	Tiller Development After Fire.....	26
2.2.3.4	Inflorescence Production Responses to Fire .....	27
2.2.3.5	Recovery Following Fire.....	28





2.3 LITERATURE CITED .....	30
<b>3 DEFOLIATION IMPACTS ON <i>FESTUCA CAMPESTRIS</i> PLANTS EXPOSED TO WILDFIRE.....</b>	<b>38</b>
3.1 INTRODUCTION.....	38
3.2 MATERIALS AND METHODS .....	41
3.2.1 <i>Site Description</i> .....	41
3.2.2 <i>WildFire Description</i> .....	42
3.2.3 <i>Experimental Design</i> .....	43
3.2.4 <i>Analysis</i> .....	45
3.3 RESULTS AND DISCUSSION.....	46
3.3.1 <i>Harvested Phytomass</i> .....	46
3.3.2 <i>Plant Height</i> .....	48
3.3.3 <i>Tiller Development</i> .....	50
3.3.4 <i>Etiolated Growth</i> .....	53
3.3.5 <i>Tiller and Plant Phytomass</i> .....	54
3.3.6 <i>Inflorescence Production</i> .....	57
3.4 CONCLUSIONS AND MANAGEMENT IMPLICATIONS.....	59
3.5 LITERATURE CITED .....	62
<b>4 RESPONSE OF <i>FESTUCA CAMPESTRIS</i> TO HEAT INJURY.....</b>	<b>74</b>
4.1 INTRODUCTION.....	74
4.2 MATERIALS AND METHODS .....	79
4.2.1 <i>Experimental Approach</i> .....	79
4.2.2 <i>Measurements and Survival</i> .....	83
4.2.3 <i>Analysis</i> .....	84



4.3 RESULTS AND DISCUSSION.....	84
4.3.1 <i>Tiller Mortality</i> .....	84
4.3.2 <i>Tiller Leaf Growth</i> .....	85
4.3.3 <i>Festuca campestris Plant Tiller Response</i> .....	87
4.3.4 <i>Festuca campestris Plant ANPP Response</i> .....	90
4.4 CONCLUSION.....	91
4.4 LITERATURE CITED .....	93
<b>5    SYNTHESIS .....</b>	<b>101</b>
5.1 LITERATURE CITED.....	108
<b>APPENDIX 1 .....</b>	<b>109</b>





## List of Tables

Table 3.1 Composition of major plant species in the exclosure at Stavely, Alberta.....	65
Table 3.2 Pedon description of the Orthic Black Chernozemic soil within the exclosure examined at AAFC sub-station near Stavely, Alberta.....	65
Table 3.3 Winter (January to March, November, December), monthly growing season, and 40-year average precipitation on the Fescue Prairie AAFC sub-station near Stavely, Alberta, from 1997 to 2000.....	66
Table 3.4 Observed F-ratio significance levels for height and phytomass changes of <i>Festuca campestris</i> plants in September of 1999 (the year of spring wildfire and defoliation treatments) and one year later in September of 2000 .....	67
Table 3.5 Observed F-ratio significance levels for etiolated growth per tiller (May), percent seedheads (July) and tiller numbers (September) of <i>Festuca campestris</i> plants in 1999 (the year of spring wildfire and defoliation treatments) and 2000 .....	67
Table 3.6 Phytomass harvested from <i>Festuca campestris</i> plants (N=120) during the first growing season following a spring wildfire and different seasons and intensities of defoliation in 1999.....	68
Table 3.7 Multivariate analysis of variance for repeated measures of height (May - July - September 2000) and percent change in tiller numbers (September 1999 – May – July – September 2000) of <i>Festuca campestris</i> plants (N=96) .....	69
Table 3.8 Mean height and phytomass of <i>Festuca campestris</i> plants (N=96) measured in September 2000, following spring wildfire and defoliation at two intensities in 1999.....	69
Table 3.9 Year-end (September) tiller counts of <i>Festuca campestris</i> plants in 1999 (N=120) and 2000 (N=96) after spring wildfire and defoliation on three dates in 1999.....	70
Table 3.10 Mean accumulated etiolated growth of <i>Festuca campestris</i> plants in May 2000 following burning and defoliation at different dates in 1999.....	70
Table 3.11 Phytomass produced for burned and unburned <i>Festuca campestris</i> plants (N=96) in September 2000, following defoliation in 1999 during either May, July, or September.....	71
Table 4.1 Analysis of linear, quadratic and cubic trends within the tiller growth data for a series of contrasts in Experiment 1.....	95



Table 4.2 Analysis of linear, quadratic and cubic trends within the tiller growth data for a series of contrasts in Experiment 2.....	95
Table 4.3 Observed F-ratio significance levels for tiller number, height, plant and tiller phytomass of <i>Festuca campestris</i> plants at the end of the monitoring period .....	96
Table 4.4 Number of tillers, mean plant height, standing crop (at the end of the monitoring period) and accumulated phytomass of <i>Festuca campestris</i> plants 14 weeks following heat treatment.....	96
Table 4.5 Change in <i>Festuca campestris</i> plant tiller numbers from pre-treatment, final plant phytomass (at the end of the monitoring period), and accumulated phytomass per tiller, as measured at the end of monitoring 14 weeks following heat treatment.....	96





## List of Figures

Figure 3.1 Mean height (+SE.) over three seasons in 2000 of burned and unburned <i>Festuca campestris</i> plants (N=96).....	71
Figure 3.2 Mean height (+SE) over three seasons in 2000 of <i>Festuca campestris</i> plants (N=96) receiving intense (5cm-stubble height) and light (15cm-stubble height) defoliation treatments in 1999.....	72
Figure 3.3 Percent change in tiller number (+SE) of <i>Festuca campestris</i> plants (N=96) between Sept 1999 and Sept 2000 during each of three periods following clipping to 5 cm- and 15 cm-stubble heights.....	72
Figure 3.4 Seasonal percent change in tiller number (+SE) of burned and unburned <i>Festuca campestris</i> plants (N=96) between Sept 1999 and Sept 2000, during each of three periods.....	73
Figure 3.5 Relative proportion of reproductive tillers (+SE) of burned and unburned <i>Festuca campestris</i> plants (N=96) in July 2000, following fire and defoliation at three different dates in 1999.....	73
Figure 4.1 Heated water treatment apparatus for laboratory experiments.....	97
Figure 4.2 Percent survival of <i>Festuca campestris</i> tillers following various exposure times at 60 °C.....	97
Figure 4.3 Growth of <i>Festuca campestris</i> tillers for longer exposure times (1-10 min.) at various temperatures in Experiment 1.....	98
Figure 4.4 Growth of <i>Festuca campestris</i> tillers ( $\pm$ S.E.) following exposure to various temperature treatments in Experiment 1.....	98
Figure 4.5 Growth of <i>Festuca campestris</i> tillers for shorter exposure times (4-32 sec.) at various temperatures in Experiment 1.....	99
Figure 4.6 Growth of <i>Festuca campestris</i> tillers ( $\pm$ S.E.) following exposure to various temperature treatments in Experiment 2 .....	99
Figure 4.7 Tiller numbers of <i>Festuca campestris</i> plants (N=80) subject to 40 or 60°C temperature treatments and defoliated at various times, as measured throughout the 14-week monitoring period. Pre-treatment (heated water bath) tiller numbers are also included.....	100



## 1 Introduction

Many natural forces have shaped biotic communities into what exists today. Of those forces, fire has been an important ecological process throughout plant evolution (Daubenmire 1968). Most terrestrial ecosystems are adapted to fire, particularly where wildfire has been prevalent in the past. Fire frequency varies across ecosystems and is influenced by regional climate and vegetation. In circumpolar taiga rangelands, wildfire frequency ranges widely from one fire per millennium to one fire per decade or less (Wein and MacLean 1983). Fire every 20-40 years in Northern Wisconsin helped to maintain the open nature of Pine Barrens by retarding woody growth, while fire every 10 years or less promoted vigorous herbaceous growth (Vogl 1974). In western Canada's prairie ecosystems, fire return intervals are relatively frequent, ranging from less than 5 years in the Tallgrass Prairie, to over 15 years in the Dry Mixed Prairie (Wright and Bailey 1982).

Fire is an important ecological process, limiting encroachment by woody species, facilitating plant community renewal by removing excessive standing dead material and litter, and recycling nutrients. Under protection from fire, areas that have historically consisted of grassland or open prairie savanna have experienced an increase in the cover of woody vegetation (Bailey and Wroe 1974, Vogl 1974, Bock and Bock 1984). Many plant communities require fire to rejuvenate growth and retrogress species composition to an earlier seral stage (Dix 1960, Anderson and Bailey 1980, Wright and Bailey 1982, Antos et al. 1983, Jourdonnais and Bedunah 1990, Redmann et al. 1993). In areas where the rate of litter accumulation exceeds decomposition with plants curing and dying back





each year, fire acts as a mechanism for accelerating the recycling of nutrients back into soil (Kramer 1973, Wright 1974, Ohr and Bragg 1985).

The Fescue Prairie of southwestern Alberta, dominated by *Festuca-Danthonia* grasslands, originally occupied the transition zone in the region south of Calgary between Rocky Mountain forests and Mixed Prairie (Moss and Cambell 1947, Looman 1969). The topography of these native rangelands varies from steep foothills to gently sloping terraces, with occasional flat valley bottoms. Foothills rough fescue (*Festuca campestris* Rydb.) is a valuable grass in the region both economically and ecologically. Ranchers rely on it extensively to provide an economical and practical source of fall and winter grazing (Willms et al. 1993, Freeze et al. 1999). Native ungulates are also dependent on rough fescue winter range for forage, as are small mammals and birds for providing cover and structure.

In the Fescue Prairie of Alberta, historical fire frequencies were 5-10 years (Wright and Bailey 1982). Over the past 100 years, the Fescue Prairie has been altered from its original expanse into smaller, more fragmented tracts that are substantially influenced by activities such as intensive agriculture, settlement and intensive land use on the surrounding landscape (Coupland 1992). One of these influences is fire suppression, implemented for the protection of natural resources and human safety. Fire suppression likely began in Alberta at the time of European settlement.

Coupled with landscape fragmentation, fire suppression has resulted in long periods without fire, enhancing the risk of more severe fires by lengthening fire return intervals and increasing fuel accumulation during the burn intercession. More recently, however, there has been an escalation in the number of wildfire events in the region,



including several small- and large-scale fires. From January of 1997 through August of 2000, a minimum of 8 wildfires were documented in the region affecting nearly 33,500 ha, with at least 5 covering areas greater than 400 ha (Bork et al. 2000).

Fescue Prairie landscapes, as influenced by historical fire and bison grazing events, existed as a mosaic of seral communities, each with unique histories of disturbance. These disturbances created more xeric environmental conditions that maintained Fescue Prairie in an area susceptible to encroachment by woody species (Romo 1996). Considerable research has been conducted into the restoration of fescue grasslands in western Canada. However, the majority of this research has been done in the Aspen Parkland (e.g., Bailey and Anderson 1978, 1980, Redmann 1978, Anderson and Bailey 1980, Romo et al. 1993, Redmann et al. 1993, Gerling et al. 1995).

Despite the importance of foothills rough fescue in southwestern Alberta, little scientific information is available on its specific response to fire, nor on how livestock grazing should be modified to facilitate its recovery. This is particularly important given that a number of studies have demonstrated the genetic and morphological uniqueness of this species (Pavlick and Looman 1984, King et al. 1995, Aiken and Darbyshire 1990) in relation to the more intensively researched, plains rough fescue (*Festuca hallii* (Vasey) Piper).

Within ranching communities of southwestern Alberta, there has also been concern expressed regarding the recovery of foothills rough fescue within burned areas, particularly given its commercial and practical importance in supporting livestock and wildlife (Willms et al. 1993, Freeze et al. 1999). Consequently, new research is being conducted to evaluate the specific susceptibility of foothills rough fescue to fire damage.





In addition, appropriate grazing management strategies need to be developed that will maximize the recovery of foothills rough fescue following fire, and ensure the long-term conservation of this key species.

To achieve this, three experiments were conducted. In the first, a field clipping study was carried out on foothills rough fescue plants burned by wildfire to determine how the timing and intensity of defoliation influences plant recovery. In the second investigation, controlled laboratory studies were used to evaluate the sensitivity of foothills rough fescue to damage under exposure to different heat temperature treatments. The third experiment was another laboratory study designed to bridge the first two. Controlled heat treatments and clipping of plants was used to explore more fully the autecological response of foothills rough fescue exposed to temperature stress and subsequent defoliation. Collectively, this information should not only lead to a greater understanding of the specific sensitivity of foothills rough fescue to heat damage, but also to the development of practical grazing guidelines for ranchers on how to ensure recovery of burned fescue rangelands.



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## 2 Literature Review

### 2.1 Fescue Grasslands

Rough fescue grasslands occupy a transition zone from open Mixed Prairie in the southern plains to forested regions in the north and west. This region forms an arc from the Aspen Parkland of central Saskatchewan extending westward into Alberta, and south along the foothills of the Rocky Mountains into the northern part of Montana (Coupland 1992). Fescue grasslands, as first described by Moss (1932), were considered a ‘submontane’ type of the Mixed Prairie by Clement and Clement (1939). Moss and Campbell (1947), however, made the distinction between these two regions by recognizing rough fescue (*Festuca scabrella* Torr.) as the dominant species in the submontane.

#### 2.1.1 Climate

Fescue grasslands in western Canada occur over a gradient of increasing elevation from east to west, resulting in varied climate. North of the Mixed Prairie, on the fringe of the Aspen Parkland in central Saskatchewan, rough fescue grasslands occur at an elevation of 500 m with a mean annual precipitation of 400 mm (Coupland 1992). In southwestern Alberta, Fescue Prairie occurs at a range of elevations from 930 m to 1950 m and greater (Moss 1944, Looman 1969). Increased elevation relative to the Mixed Prairie to the east increases precipitation and results in cooler summer temperatures. Annual precipitation averages 445 mm for the Fescue Prairie Ecoregion (Strong and Leggat 1992). The overriding climatic characteristic of the Fescue Prairie is the influence of a pronounced continental climate, with short, moderately warm summers and long,



cold winters where most of the precipitation falls in May and June (Strong and Leggat 1992). Mean summer temperatures are 14°C and winter temperatures are frequently moderated by chinook conditions causing snow to disappear.

### *2.1.2 Geomorphology and Soils*

Glacial deposits of Pleistocene age cover most of the region as a result of advance and retreat of the Laurentide ice sheet. The landscape on the plains of this region is expressed as rolling, hummocky till, a heterogeneous, non-bedded mixture of rock material of all sizes (Moss 1944). In the Fescue Prairie along the foothills, the effects of glacial ice are less pronounced in terms of major landscape changes than in the adjacent prairies or mountains (Beaty 1975). Alteration by non-glacial forces, principally post-glacial streams and rivers formed much of the landscape in the foothills that predominates today.

Foothills rough fescue grasslands typically coincide with Black Chernozemic soils (Moss and Campbell 1947), and are indicative of development under cool, subhumid conditions found in the northern interior plains of western Canada. Soils found under foothills rough fescue grassland in southwestern Alberta are considered highly productive. Surface horizons are darkened by the accumulation of organic matter from the decomposition of mesophytic grasses and forbs representative of grassland communities or grassland-forest communities with associated shrubs and forbs.

The occurrence of fescue grasslands in a prairie-forest transition zone influences soils and vegetation of the area through a pattern of historical advance and retreat of trees (e.g., *Populus tremuloides* Michx., *Pseudotsuga menziesii* (Mirb.) Franco) and associated





shrubs (e.g., *Salix* spp.). Fire suppression and bison (*Bison bison bison* Linnaeus.) extirpation are believed to have allowed shrub and tree invasion into fescue grasslands (Johnston and Smoliak 1968, Bailey and Wroe 1974, Scheffler 1976, Fuller and Anderson 1993, Campbell et al. 1994). There is also evidence that forest encroachment onto grasslands causes soil eluviation through increased acidity (Dormaer and Lutwick 1966, Lutwick and Dormaar 1968, Fuller and Anderson 1993). If aspen trees persist, the soil will eventually be transformed into a Dark Gray Chernozem and ultimately, to a Luvisol. Dormaar (1971) found that only 2-3 years of simulated aspen leaching is needed to change soil chemical and physical properties. There is an associated decrease in soil pH and loss of organic matter with aspen forest encroachment (Dormaer and Lutwick 1966). The degree to which Black Chernozemic soils are altered by forest invasion is affected by microrelief on the landscape (Fuller and Anderson 1993).

Reintroducing fire to the landscape has been investigated as a means of altering the relative cover of forest and grassland. Single fire events have been found to increase the relative density of woody species (Anderson and Bailey 1979). However, burning these areas annually has kept tree and shrub cover at pre-settlement levels (Anderson and Bailey 1980). An effective method of limiting forest expansion and promoting herbaceous growth has been the use of spring fire followed by late season grazing (Bailey et al. 1990).

### 2.1.3 Fescue Prairie Types

Currently, Strong and Leggat (1992) differentiate between the Fescue Prairie Ecoregion in southwestern Alberta lying west of the Mixed Prairie Ecoregion in an



elevational transition to the foothills, from plains rough fescue grasslands occurring at lower elevation in the Aspen Parkland of the northern plains (Appendix 1). Fescue Prairie is also marked by the dominance of foothills rough fescue (*Festuca campestris* Rydb.) rather than plains rough fescue (*Festuca hallii* (Vassey) Piper). Regardless of the cartographic and geographic classification of Fescue Prairie throughout western Canada, geographic and topographic changes in all areas affect species composition and create different potential natural communities in which the relative dominance of rough fescue or its co-dominant species vary.

#### 2.1.3.1 *Festuca campestris* Rydb. – *Danthonia parryii* Scribn. Range Type

On undisturbed mesic uplands in southwestern Alberta, *F. campestris* dominates vegetational cover, growing nearly to the exclusion of other grasses and forbs. On grazing exclosures in the lower southern foothills, Wroe (1971) reported *F. campestris* as having a canopy cover of 94%, representing approximately 75% of the total herbage phytomass. Exposure of these systems to natural variability in growing conditions and disturbance is more likely to result in the co-dominance of rough fescue with another grass species, with this second species having 12 to 15% of total plant density (Looman 1969). In the Fescue Prairie of southwestern Alberta, the combination of foothills rough fescue and Parry oat grass predominates (Moss and Campbell 1947, Moss 1955, Looman 1969). Subdominants of this range type include *Festuca idahoensis* Elmer, *Stipa columbiana* Macoun, *Agropyron spicatum* (Pursh) Scribn. & Smith, *Achillea millefolium* L., *Potentilla fruticosa* L. and *Salix* spp. L. (Moss and Campbell 1947). Fescue Prairie is





more species rich in forbs than the Mixed Prairie, and in general, is greater in species richness relative to other prairie ecosystems (Coupland 1992).

In southwestern Alberta, components of the Palouse Prairie (e.g., *Agropyron spicatum*) are also found to extend eastward through the mountains contributing to the diversity in the area (Moss and Campbell 1947, Moss 1955). The *Agropyron spicatum* range type is primarily found on the more xeric south-facing slopes of the lower foothills. On north-facing slopes and at higher elevations, there is potential for succession to wooded vegetation. At lower elevations, *Festuca-Danthonia* communities are susceptible to invasion by willow, followed by poplar and in turn, to white spruce (*Picea glauca* [Moench] Voss), while at higher elevations, lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) and Douglas-fir (*Psuedotsuga menziesii* Franco Mirb.) may encroach these grasslands (Moss and Campbell 1947).

#### 2.1.3.2 *Festuca hallii* (Vassey) Piper – *Stipa curiseti* A.S. Hitchc. Range Type

This is the dominant potential natural community of the Aspen Parkland region along the southern fringe of the boreal forest in central Alberta and Saskatchewan (Coupland and Brayshaw 1953). As with *F. campestris* in the foothills, *F. hallii* is capable of forming more than 50% of the vegetative cover on mesic sites (Coupland 1992), but more often co-dominates with *S. curtiseti* (Coupland and Brayshaw 1953). Many subdominant plants occur on a variety of sites with *F. hallii*, including *Agropyron subsecundum* (Link) A.S. Hitchc., *Agropyron dasystachyum* (Hook.) Scribn., *Solidago* spp. and upland *Carex* spp. (Sinton 1980). On more xeric sites *Stipa curtiseti*, *Agropyron* spp., and *Bouteloua gracilis* (HBK) Lag. dominate (Sinton 1980).



Aspen Parkland was once dominated by open fescue grassland, with pockets of aspen groves and white spruce or lodgepole pine further north near the transition into the boreal region (Bailey and Wroe 1974). *Eleagnus commutata* Bernh. ex Rydb. and *Symphoricarpos occidentalis* Hook. occur on more mesic sites and often precede invasion onto grassland by aspen (Bailey and Wroe 1974). Coupland and Brayshaw (1953) considered the grassland component to be a preclimax of *Populus* forest. Strong and Leggat (1992) document two subregions in the Parkland, including a drier southern region where the area of aspen in the landscape may be as low as 3%, and a northern region where aspen is more common.

#### 2.1.4 Ecology and Use

Fescue grasslands provide opportunities for economical and sustainable livestock grazing, as well as other important values such as ecosystem conservation, watershed properties, wildlife habitat, recreational opportunities and aesthetics. Its use and management today for sustainable production is fundamentally reliant on the natural history of disturbance. Historically, fescue grasslands were undoubtedly influenced by the foraging of many wildlife species, the most prevalent of those likely being plains bison which routinely wintered in the Fescue Prairie and Aspen Parkland Ecoregions following seasonal migration from the Mixed Prairie (Morgan 1980). This migration to fescue grasslands was driven largely by the availability of a sufficiently high-energy winter diet and a protein-rich spring diet. Bison forage selection and behavioural traits such as trampling, wallowing and rubbing helped shape the character of fescue grasslands. By implementing management practices that mimic natural disturbance



history, any negative impacts caused by cattle grazing can be minimized and the quality of fescue grasslands enhanced (Baumeister et al. 1996).

The adaptation of foothills fescue grassland to grazing while plants are dormant makes the species well suited to winter grazing, but these areas are usually managed using a system of continuous cattle grazing during summer (Willms et al. 1986). Cow condition can be maintained by grazing fescue grasslands in the fall (Willms et al. 1993), but nutrients drop below the minimum required for maintenance through winter (Johnston and Bezeau 1962). To ensure adequate cow condition for calving and rebreeding in spring, the most economical option for cattle producers in this region is to supplement the diet of cattle grazing on fescue grassland (Freeze et al. 1999).

## **2.2 Rough Fescue**

### *2.2.1 Taxonomy*

The taxonomy of rough fescue has changed over the years. The *Festuca* genus is widespread, occurring in eastern Asia and North America (Pavlick and Looman 1984). Three species of rough fescue occur in Canada and adjacent parts of the United States, northern rough fescue (*Festuca altaica* Trin.), foothills rough fescue (*F. campestris*), and plains rough fescue (*F. hallii*) (Pavlick and Looman 1984, Aiken and Gardiner 1990). This is the most recent division in what has been a century of debate.

Rough fescue was first described in North America in 1829 based on its morphological similarity to *F. altaica* material from central Asia (Pavlick and Looman 1984). Although geographically distinct (Looman 1982, Hill et al. 1997), the rough fescue complex has been considered morphologically similar enough to be a single





species. Rough fescue has been classified as geographic variants of *F. altaica* (Scoggan 1978) or as subspecies of *F. scabrella* (Johnston 1958, Harms 1985).

Johnston and Crosby (1966) distinguished plains and foothills forms of rough fescue based on the more frequent occurrence of rhizomes in the plains variety. They presumed under drier edaphic conditions, *F. scabrella* (referring to the southern variety of *F. altaica*) tends to assume a bunched growth form, while in mesic situations and on more favourable soils, the creeping-rooted habit is more prevalent. This distinction was also based on material of the tufted and rhizomatous forms that were collected from geographically distinct areas. The description of the growth forms of plains and foothills rough fescue coincides with other investigator's distinction of the two species based on growth characteristics (Pavlick and Looman 1984, Aiken and Darbyshire 1990), in that moister conditions lead to the rhizomatous nature of *Festuca*. In reality, the region in which *F. hallii* grows is often drier than the foothills region, the habitat of *F. campestris* (Strong and Leggat 1992), indicating that effective moisture may differ from actual precipitation and be important in the development of morphological characteristics. Although untested, it is also possible that morphological differences originate from regional adaptations to unique fire or grazing regimes.

The geographic distribution of each of the three fescue species has lent to their separation. *F. campestris* is predominantly found in the foothills of southwestern Alberta, *F. hallii* occurs in a belt of the northern parkland from central Manitoba to west-central Alberta, and both species are found in the Cypress Hills of southeastern Alberta (Looman 1982). *F. altaica* generally occurs at high elevation in subalpine and alpine regions of the Rocky Mountains and at more northern latitudes in Alberta, British



Columbia and the Yukon (Looman 1982). Based on differences in growth response to temperature (King et al. 1995), morphological characteristics (Looman 1982, Pavlick and Looman 1984, Aiken and Lefkovitch 1984, Aiken and Gardiner 1990, Aiken and Darbyshire 1990) as well as knowledge-based and inductive modeling of rough fescue distribution (Hill et al. 1997), these three species are now recognized separately.

### *2.2.2 Grazing Effects on Rough Fescue*

#### 2.2.2.1 Soil Changes

The relative intensity of grazing can affect the function of soils under rough fescue grassland and its ability to support plant growth. Alteration of soil characteristics can occur as a result of grazing influences on watershed and nutrient cycling (Naeth et al. 1991). After more than 20 years of very heavy grazing (4.8 AUM/ha) the upper portion of the Ah horizon was degraded from a black soil (10 YR 2/1) coinciding with light grazing pressure (1.2 AUM/ha), to a dark brown soil (10YR 3/3) (Johnston et al. 1971, Dormaar and Willms 1990, Dormaar and Willms 1998). This change is associated with a loss of soil organic matter as a result of decreased litter available for decomposition and incorporation into the soil (Naeth et al. 1991).

Litter reduction under high intensity grazing, coupled with less desirable soil conditions (e.g., increased bulk density and reduced hydraulic conductivity) increases the potential for severe run-off, erosion and evaporation (Dormaar et al. 1989, Naeth et al. 1991, Naeth and Chanasyk 1996). Imbalances in soil fertility (e.g. increased soil nitrogen and decreased phosphorous) and decreased water holding capacity of the soil put the long-term sustainability of rough fescue soils at risk (Dormaar and Willms 1998).



Reductions in organic matter and the breakdown of soil structure contribute to soil surface sealing, reduced infiltration rates and increased evaporation, which in turn exacerbates changes in the plant community caused by intensive grazing (Dormaer and Willms 1990, Dormaar and Willms 1998). Prolonged heavy grazing transforms soil to that is indicative of a drier microclimate with associated changes in plant species tolerant of the warmer, drier soil conditions (Johnston 1961, Dormaar and Willms 1990, Dormaar and Willms 1998).

#### 2.2.2.2 Fescue Grassland Vegetational Response to Grazing

Rough fescue community composition is influenced by the history and severity of disturbance. The dominance of rough fescue in vegetative cover can be an indicator of the extent of these disturbances (Moss and Campbell 1947, Coupland and Brayshaw 1953, Vujnovic et al. 2000). Increases in grazing pressure results in dominance of species that are less favoured by livestock (Willms and Rhode 1998) and hence are more resistant to grazing (Dormaer and Willms 1998). Under moderate to very heavy grazing, the amount of bare ground has been found to increase in foothills fescue grassland (Naeth et al. 1991). The removal of litter and exposure of mineral soil as a result of excessive grazing are the apparent mechanisms for species change (Vujnovic et al. 2000), as grazing may lead to more shallow-rooted and less productive species (Dormaer and Willms 1998).

Changes in plant community composition can occur along an edaphic or grazing intensity gradient. For instance, there is generally a decline in rough fescue cover and an increase in the proportion of Parry oat grass and Idaho fescue in climax (e.g., ungrazed)





communities as site conditions become drier due to steep slopes, gravelly or shallow soils (Willoughby et al. 1997). A reduction of rough fescue, however, can also occur within a *Festuca-Danthonia* range type as a result of grazing. As grazing pressure increases to high levels, Parry oat grass also decreases and shorter, less palatable forbs such as *Artemisia frigida* Willd., *Oxytropis campestris* (L.) DC. var *gracilis* (A. Nels.) Barneby, *Taraxacum officinale* Weber and upland sedges (*Carex* spp.) increase (Willms et al. 1985). With sustained heavy grazing, mesic sites typically dominated at climax by a *Festuca-Danthonia* range type will retrogress to a Timothy (*Phleum pratensis* L.) – Kentucky bluegrass (*Poa pratensis* L.) / Dandelion type (*Taraxacum officinale*) with an associated loss or reduction in native species (Willoughby et al. 1997). Greater resistance of exotic species such as Kentucky bluegrass, to intense, repeated defoliation leads to their invasion and dominance (Looman 1969), with invasive species dominating the soil seed bank under these conditions (Willms and Quinton 1995). Soil disturbance may also lead to a seral community dominated by annual forbs, rather than rough fescue (Willms and Quinton 1995). Lowland areas tend to be more prone to retrogression as these areas have the most available forage and therefore, the highest utilization rates by cattle early in the growing season when native plants are most susceptible to grazing (Willms 1988b). Rough fescue can be nearly eliminated under very high grazing pressure, but light grazing pressure has no apparent affect on range condition as reflected by botanical composition (Willms et al. 1985). A recovery time of approximately 30 years has been suggested for overgrazed rough fescue rangelands to return to excellent condition (Maclean and Tisdale 1971, Willms et al. 1985).



In the absence of disturbance, the ability of rough fescue to initiate growth early in the season and accumulate litter makes it a strong competitor and capable of excluding other species and decreasing species richness (Vujnovic et al. 2000). Under protection from grazing, the dominance of rough fescue leads to a simplification of flora (Johnston 1961). Biodiversity can be increased by grazing in grassland ecosystems that have experienced a reduction in populations of keystone species or a decline in species richness due to anthropogenic stresses (Collins et al. 1998). This is also true of the Fescue Prairie, in which the greatest species diversity is usually achieved at an intermediate level of disturbance (Willoughby 1992, Bork 2000, Bai et al. 2001).

#### 2.2.2.3 Rough Fescue Plant Response to Grazing

The accumulation of excessive litter in the absence of grazing is capable of reducing the productivity of grasslands either by insulating the soil, lowering the rate of mineral recycling or accumulating allelopathic toxins in litter (Rice and Parenti 1978). Removal of standing dead plant litter from *Festuca* grasslands for 2-3 consecutive years resulted in yields that were marginally greater (Sinton 1980, Willms et al. 1986). Plant vigour was also enhanced with dormant season grazing by stimulating tillering in rough fescue plants, indicating this may be responsible for the increased production potential (Willms et al. 1986). A single defoliation in fall does not affect yield from rough fescue grasslands (Johnston 1961).

An increase in tillering of rough fescue plants is commonly observed as a result of either defoliation in the dormant season or the removal of litter (Willms et al. 1986, Willms 1988a, Gerling et al. 1995). Asexual reproduction in rough fescue is important



for propagation and sustained production of the plant as old tillers in the center of the plant die. Initiation of tillers from axillary buds may occur as a result of changes in the plant environment or changes within the plant itself. The concept of tiller initiation being regulated by apical dominance due to hormonal interaction between the apical meristem and axillary meristems may not be substantiated (reviewed by Murphy and Briske 1992). A number of environmental conditions including radiation quality and quantity, photoperiod, resource availability, temperature, and competition are known to influence tiller initiation in grasses (Langer 1963, Laude 1972, Willms 1988a, King et al. 1995). In general, tillering is optimized as environmental conditions become more conducive to plant growth. Tillering is promoted with a lower temperature regime representative of spring and fall temperatures and increased photosynthetically active radiation (PAR) penetrating the crown of the plant (Langer 1963, Willms 1988a, King et al. 1995). Tillering rates tend to decrease with reductions in soil water content (Langer 1963, Willms 1988a). In many instances an increase in tiller density is associated with a decrease in plant height (Willms 1988a, Willms and Fraser 1992, Gerling et al. 1995). When coinciding with an increase in tillering, a reduction in plant height is likely a response to more competition for resources among a greater number of tillers (Willms 1988a).

Defoliation of rough fescue plants in the growing season can be detrimental, as evidenced by reduced yields, decreased etiolated growth, plant height and tiller number per plant (Willms 1988a, Willms 1991, Willms and Fraser 1992). Repeated intensive defoliation of rough fescue plants early in the growing season on rangelands in B.C. resulted in plant mortality (McLean and Wikeem 1985). In contrast, 80% utilization





annually over a 32-year period failed to completely eliminate rough fescue plants from fescue grasslands in southwestern Alberta (Willms et al. 1985). Regardless, rough fescue's sensitivity to grazing in the growing season suggests fall or winter grazing is more sustainable (Willms 1991, Willms and Fraser 1992). Not surprisingly, this follows the natural evolutionary history of grazing in rough fescue grasslands, which were grazed predominantly in the dormant season (Morgan 1980).

The most apparent reason for the negative response of rough fescue to defoliation in the growing season is carbohydrate transfer from roots to green photosynthetic material. Plants furnish above-ground growth at the expense of carbohydrate reserves in the roots and crown (Avigad and Dey 1997). Rough fescue plants experience reductions in etiolated growth, a reflection of carbohydrate levels in the roots and crowns of plants (Drovat et al. 1972), following defoliation in the growing season (Johnston 1961, Willms and Fraser 1992). Plants may be particularly susceptible to tiller mortality and decreases in carbohydrate reserves during the flowering stage due to increased demand for nutrients by the reproductive tillers (Ong 1978). Energy removal from the plant sets back growth substantially. Reductions in root mass as a result of excessive grazing affect the long-term viability of the plant (Johnston 1961). The loss of deep penetrating roots decreases the ability of rough fescue plants to access soil moisture and nutrients, lowering phytomass production and leading eventually to replacement by shallow-rooted and rhizomatous exotic grasses inherently more tolerant of dry soil conditions (Bork 2000). In the case of Idaho fescue as many as 6 years without disturbance may be needed for carbohydrates to recover to previous levels (Mueggler 1975).



The infrequency with which rough fescue sets seed and the lack of a predictable mechanism for triggering floral initiation (Johnston and MacDonald 1967) makes any inferences regarding defoliation impacts on seedhead production difficult to discern. However, Gerling et al. (1995) found an increase in inflorescence production of plains rough fescue following mowing of fescue grasslands. Increased flowering among various grass genera is generally believed to occur as a result of defoliation (Daubenmire 1968). Shading of the plant crown from excessive litter accumulation can inhibit tiller initiation from axillary buds (Willms 1988a) and thus, may also inhibit the development of floral primordia.

### *2.2.3 Fire Effects on Rough Fescue*

The response of fescue grasslands to fire is variable and depends on a variety of site conditions and aspects of fire behaviour. The impact of fire on a given area will vary with time since the last fire event, grazing history, seasonality of the fire, as well as environmental conditions before, during and after burning. The most common ignition sources for wildfire are lightning and humans. The likelihood of fuels combusting, and fire behaviour, is subject to the availability and continuity of fuel, topography and climatic, mostly wind, conditions (Pyne 1996).

In fire prone areas, a description of the ecological effects of fire has useful management implications for the pre- and post-burn environment. The definition of fire intensity, as it is known today, arose out of the need to quantify fire behaviour based on known conditions to predict fire characteristics. Fire intensity became linked to mathematical models that attempted to account for environmental variables causing fires



to burn hotter, flame higher or move faster. The mathematical model developed by Byram (1959) calculates fire intensity as a function of rate of energy or heat release per unit time per unit length of fire front [ $I = Hwr$ ; where  $I$ =fire intensity ( $\text{kW m}^{-1}$ ),  $H$ =heat yield of the fuel ( $\text{kJ kg}^{-1}$ ),  $w$ =weight of available fuel ( $\text{kg m}^{-2}$ ), and  $r$ =rate of spread ( $\text{m sec}^{-1}$ )]. Information available from this model is likely more useful in terms of fire suppression efforts and effect on plant propagules above the flames than it is for describing the impact on understory or grassland vegetation (Feller 1998). As fire intensity is strongly influenced by rate of fire spread and combustion properties of the fuel burned, it describes the instantaneous heat release by the flaming front of a fire line (Tangren 1976). However, heat release is not confined to the passage of the fire front. Without an expression of the duration of heat released by fire for a given area, it does not adequately describe fire effects on plants.

The effect of fire on the environment is more appropriately described by fire severity. Severity generally refers to the degree of mortality or damage to living plants for above- and below-ground propagules (Ryan and Noste 1985). One of the drawbacks of using fire intensity to describe plant community responses is that the same fire intensity may not result in the same severity (damage or mortality) to plants due to various plants being more or less adapted to fire (Chapman and Crow 1981, Rowe 1983). The risk of plant mortality or injury is generally a function of the time – temperature relationship of heat that sensitive plant parts are exposed to during fuel consumption (Hare 1961, Yarwood 1961, Wright 1970). Again, fire intensity is an inadequate descriptor of fire for assessing fire effects on plants, as the same fire intensity may cause





consumption of different proportions of surface fuel, ground and organic fuel (Finney and Martin 1991).

Fire severity, particularly in grasslands, is useful for describing the impact of fire on vegetation, but has variable connotations depending on the environment it is applied to and the method of measurement. Plant community adaptation to fire, surface, ground and organic fuel consumption, maximum soil surface temperatures, and heat flux into the soil have all been used to describe fire severity (e.g., Woodard 1977, Hartford and Fransden 1992, Agee 1993, Schimmel and Granstrom 1996, McDaniel et al. 1997, Archibold et al. 1998, Morgan 1999, Preisler et al. 2000).

In the Fescue Prairie of southwestern Alberta, direct effects of fire on rough fescue plants can be observed through a measure of plant mortality. It is the burning of fescue crowns and damage to growing points that causes mortality to plants (Bailey 1978, Wright and Bailey 1982). Mortality of rough fescue is often postulated to be a result of greater accumulations of litter as a result of protection from fire and grazing (Antos et al. 1983, Bork et al. 2000). Jourdonnais and Bedunah (1990) observed that in areas of heavy litter accumulation, rough fescue plants smoldered for as long as 20 minutes after the passage of the fire front. The tendency of rough fescue plants to increase in basal area (Johnston 1961) and accumulate litter with age results in large-bunched fescue plants being more damaged than small ones during fire (Antos et al. 1983). Antos et al. (1983) found tiller recruitment tended to decrease with increasing bunch size of rough fescue plants exposed to fire possibly due to increased fire severity effects. In the Tallgrass Prairie of Kansas, bunchgrasses decreased more in basal area and production in locations with greater fine fuels prior to burning (Ewing and Engle 1988). Observations of fire in



the field may indicate that rough fescue tillers die as a result of extended periods of high temperature next to bunches, but this has yet to be determined conclusively. Ultimately, there are many factors that influence the resistance and recovery of a plant exposed to fire.

#### 2.2.3.1 Microclimate Changes Following Fire

Reduced vigour as a result of direct injury to the plant during fire is difficult to assess because changes in the microclimate following fire may decrease plant cover, production, or height. A greater soil temperature following fire is commonly found in fescue grasslands (e.g., Antos et al. 1983, Redmann et al. 1993, Gerling et al. 1995). The moderating effect that litter has on grassland soil temperature is lost when this layer is removed by fire. Soil temperatures are also generally more variable (e.g., higher during the day and lower at night) on burned areas in grasslands (Savage 1980). The location of tiller buds and shoot apices near the soil surface in bunchgrasses means their growth will be affected by soil temperature (Rice and Parenti 1978).

An increase in soil temperature is the result of greater net radiation at the soil surface due to litter removal and a blackened surface (Redmann et al. 1993). Greater evaporation rates due to the warmer, darker soil surface may create drought-like conditions. Increased soil temperature may further exacerbate drought by decreasing soil water viscosity, which increases percolation and lowers field capacity (Savage 1980). There is an increased risk of soil erosion associated with exposed soil that has undergone such changes in physical properties (Naeth et al. 1991).



With the loss of insulating cover and standing dead litter there is also an increase in wind speed at the ground surface on burned areas (Old 1969, Knapp 1984). Increased wind speed contributes to greater evaporation and decreased leaf temperature. Wind-exposed plants tend to be shorter and have lower standing phytomass likely as a result of increased leaf temperature and transpiration rates (Savage 1980).

#### 2.2.3.2 Cover and Production Changes with Fire

Declines in primary production during the first growing season following fire occur in both foothills rough fescue (*F. campestris*) (Jourdonnais and Bedunah 1990, Bork et al. 2000) and plains rough fescue (*F. hallii*) communities (Redmann et al. 1993, Gerling et al. 1995). Lower phytomass production has been attributed to a reduction in cover and plants being generally shorter following fire (Bailey and Anderson 1980, Gerling et al. 1995) coupled with plant damage directly caused by the fire (Antos et al. 1983, Jourdonnais and Bedunah 1990, Bork et al. 2000). A review of fire research by Redmann (1978) revealed that a reduction in primary production following fire was mainly the result of lower plant and soil water potentials.

Water is generally the most limiting nutrient for plant growth in grasslands (Sala et al. 1988). During the winter, snow trapping is important for moisture storage and ground water recharge in the spring (de Jong and MacDonald 1975, as cited in Redmann et al. 1993). Reduced snow trapping on rough fescue grassland burned in the fall may be largely responsible for reduced soil water potentials, which in turn cause a greater negative impact on herbage production relative to spring burning (Redmann et al. 1993,





Grilz and Romo 1994). Moisture was particularly important in the study by Redmann et al. (1993), as two years of drought followed burning.

Season of burning can also influence growth response. Gerling et al. (1995) established that there is less of a decrease in phytomass and plant height and a greater increase in tillers and inflorescence production, following early spring rather than fall burning. Given that burning in both the fall and spring occurred while plants were dormant, differences between the two may have been due to plant responses having been measured over two growing seasons after the spring burn and only one after the fall burn. In general, spring fire is detrimental to plants only if growth has been initiated when fire occurs and becomes increasingly harmful as plants accumulate more new phytomass prior to burning (Bailey and Anderson 1978, Gerling et al. 1995).

#### 2.2.3.3 Tiller Development After Fire

Increases in tillering of rough fescue plants following fire have been attributed to mechanisms similar to those following defoliation, such as increased PAR at the crown of the plant (Willms 1988a, Gerling et al. 1995). As burning and mowing caused similar responses in tiller density, Gerling et al. (1995) determined that there was no intrinsic effect of fire on the plant or microenvironment that stimulated the production of tillers. In contrast, Idaho fescue has been found to decrease in tiller number as a result of burning (Robberecht and Defossé 1995). Decreases in tiller number are exacerbated by early season defoliation following fire and result in high plant mortality (Bunting et al. 1998). It was postulated that detrimental impacts were the result of a more stressful microenvironment combined with direct effects of fire and defoliation on plant



physiological processes. Tiller and plant mortality both decreased when defoliation was deferred one full growing season following fire, allowing vegetative regrowth and the recharge of stored nutrients to ameliorate harsh post-fire environmental conditions.

Initiation of vegetative tiller growth tends to occur earlier in the first (Gerling et al. 1995, Bork et al. 2000) or second (Redmann et al. 1993) growing season following fire. Warmer soil temperatures in burned areas may provide conditions more conducive to plant growth earlier in the season (Savage 1980). On the other hand, the observation may be the result of burned areas simply appearing greener due to the removal of litter (Antos et al. 1983) or due to a more intense green appearance in the leaves of grasses due to higher nitrogen concentration (Redmann et al. 1993, Bork et al. 2000). Even though tiller growth may begin earlier in the growing season on burned areas, phenological development may be delayed (Bork et al. 2000) resulting in slower growth rates (Gerling et al. 1995) and a shift in peak phytomass to later in the season (Redmann et al. 1993).

#### 2.2.3.4 Inflorescence Production Responses to Fire

Burning tends to decrease rough fescue inflorescence production in the first growing season following fire (Bailey and Anderson 1978, Gerling et al. 1995, Bork et al. 2000). Initiation of floral primordia in foothills rough fescue occurs in late August and early September, but apices are elevated to a greater extent in early spring (Johnston and MacDonald 1967). This pattern makes apices vulnerable to dormant season fire and even more sensitive once spring growth has been initiated (Bailey and Anderson 1978). An increase in inflorescence production found on rough fescue grasslands in the second growing season following fire may be a response to greater PAR levels at the plant crown



within the post-burn environment (Willms 1988a, Gerling et al. 1995, Bork et al. 2000). Annual burning may, however, eliminate inflorescence production (Anderson and Bailey 1980).

In other grass species, inflorescence production is more strongly influenced by moisture regime than fire occurrence, with an increase occurring in a mesic year following a dry year (Knapp and Hulbert 1986, McFarland and Mitchell 2000). Generally, these studies concluded that in a dry year, nitrogen is conserved or may accumulate through increased nitrification due to warmer soils, and is therefore more available the following year. Drought conditions imposed by burning may simulate this effect allowing for an increase in inflorescence production relative to unburned areas, provided moisture is not limiting during the following year.

#### 2.2.3.5 Recovery Following Fire

Rough fescue rangeland requires at least two years to recover in production to unburned levels (Antos et al. 1983, Jourdonnais and Bedunah 1990, Redmann et al. 1993, Gerling et al. 1995, Bork et al. 2000). Cover of rough fescue and associated species, which are altered by burning, usually return to pre-burn levels within three years (Bailey and Anderson 1978, Antos et al. 1983). Recovery rate is often a function of the severity of damage imposed by fire, including whether it occurred in the dormant season or while plants were actively growing (Bailey and Anderson 1978, Gerling et al. 1995). In the absence of other disturbances, precipitation following fire may also affect recovery of grasslands. Redmann et al. (1993) found that native species recovered more quickly in





growth and productivity from spring rather than fall burning, likely as a result of reduced snow trapping in the fall burn.

The longest lasting impact of fire appears to be the loss of litter in burned areas. Loss of litter is important in rough fescue grasslands as it regulates herbage production, protects soil and is slow to re-accumulate (Willms et al. 1986). Even though production and cover of rough fescue grassland on burned areas tends to be the same as unburned areas 2 to 3 years following fire, litter remains lower (Antos et al. 1983, Jourdannais and Bedunah 1990). Bork et al. (2000) found that three years after fire, although litter cover was similar between burned and unburned locations, litter biomass remained lower on burned areas.



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### 3 Defoliation Impacts on *Festuca campestris* Plants Exposed to Wildfire

#### 3.1 Introduction

Fire is a natural and integral component of grassland systems (Vogl 1974). The Fescue Prairie of southwestern Alberta is no exception, having evolved under the influence of both fire and grazing. Historical fire frequencies in this region were 5-10 years (Wright and Bailey 1982). Foothills rough fescue (*Festuca campestris* Rydb.) is the dominant climax species of grasslands throughout the region (Moss and Campbell 1947, Looman 1969). Today, foothills rough fescue provides an economical and practical source of fall and winter grazing for ranches in southwest Alberta (Willms 1993).

Grazing effects on foothills rough fescue have been well documented. Rough fescue is sensitive to defoliation during the growing season and loses competitiveness when grazed at this time (Looman 1969). Rough fescue declines in production and vigour with increased cutting frequency and decreased (e.g., shorter) cutting height (McLean and Wikeem 1985, Willms 1991, Willms and Fraser 1992). Defoliation and litter removal has been shown to decrease plant height and increase tillering in rough fescue as a result of increased photosynthetically active radiation (PAR) at the crown (Willms et al. 1988). Less desirable species replace rough fescue as it declines in cover (Moss 1955). Soils under rough fescue decline in organic matter content as a result of greater stocking rates (Johnston et al. 1971, Dormaar and Willms 1990).

Several previous studies have investigated the effect of fire on rough fescue grasslands. Most of these studies involved plains rough fescue (*Festuca hallii* (Vassey)





Piper) following prescribed burning in the Aspen Parkland of Alberta and Saskatchewan (Bailey and Anderson 1978, Anderson and Bailey 1980, Redmann et al. 1993, Gerling et al. 1995). Plains rough fescue, however, differs morphologically from foothills rough fescue (Pavlick and Looman 1984) and given that the core of their distribution dominates different geographic regions, this suggests a potentially different response to fire and grazing due to these adaptive traits.

Burning of rough fescue grasslands generally causes a decline in fescue cover (e.g., Bailey and Anderson 1978, Antos et al. 1983), and production (Jourdonais and Bedunah 1990, Redmann et al. 1993, Gerling et al. 1995, Bork et al. 2000). Investigators have found improvements in forage quality, particularly protein content, following fire in plains rough fescue (Redmann et al. 1993) and foothills rough fescue (Bork et al. 2000). Studies investigating foothills rough fescue response to fire have mostly examined changes in the plant community as a whole rather than the response of individual fescue plants (e.g., Antos et al. 1983, Bork et al. 2000). Although considerable research has addressed the combined effects of fire and livestock grazing on range plants (e.g., Barker and Erickson 1971, Wright 1974, Willms et al. 1980), relatively little is known of the cumulative effects of grazing following burning on foothills rough fescue plants.

Following settlement of the Fescue Prairie region in the early 1900's, attempts at suppressing wildfire were successful. More recently, however, there has been a noticeable increase in the number of wildfires impacting rangelands in the region. From January of 1997 through August of 2000, 8 wildfires were documented affecting nearly 33,500 ha, with at least 5 fires burning areas greater than 400 ha (B. Adams, personal communication, as cited in Bork et al. 2000). The number of wildfires affecting the area,



and their potential impact on the ranching community, has raised concerns regarding grazing management, including its implications prior to wildfire and subsequent effect on plant resilience and recovery following fire. The effects of improperly timed or excessive intensities of defoliation following fire have not been examined on rough fescue.

Defoliation may impose an additional stress on burned rough fescue plants, impeding their survival and recovery. The development of appropriate grazing guidelines will ensure rapid recovery of rough fescue after burning, as well as minimize long-term negative impacts on ranching operations.

In April of 1999, a small, localized wildfire in a climax ungrazed *Festuca campestris* – *Danthonia parryi* rangeland at the Agriculture and Agri-Food Canada research substation near Stavely, Alberta provided an opportunity to test the following specific objectives:

1. Assess wildfire impacts on foothills rough fescue plant morphological responses, including plant height, tiller numbers, seedhead production, and above-ground net primary production (ANPP).
2. Evaluate the response of foothills rough fescue to variation in the season and intensity (e.g., stubble height) of defoliation.
3. Determine important defoliation regime interactions with burning on the subsequent recovery (e.g., resilience) of rough fescue plants.



## 3.2 Materials and Methods

### 3.2.1 Site Description

The study was conducted at the Agriculture & Agri-Food Canada research sub-station near Stavely, in the Porcupine Hills of southwestern Alberta (50° 11' 30" N, 113° 53' 30" W; 1,366 m above sea level). This area is located within the Fescue Prairie ecoregion on the eastern slopes of the Porcupine Hills (Strong and Leggat 1992). Moss and Campbell (1947) describe the regional vegetation types within native Fescue Prairie.

The study was conducted in an area that experienced either no grazing or light grazing from 1949 until 1982, when it was fenced to exclude livestock. The plant community in the exclosure was a foothills rough fescue (*Festuca campestris* Rydb.) – Parry oat grass (*Danthonia parryi* Scribn.) range type (Table 3.1), indicative of the modal range type for the region (Wroe 1972, Strong and Leggat 1992). Vegetation within the exclosure was considered to be in climax condition (Willms et al. 1996). The regional landform is rolling moraine upland. The local range site has a slope of approximately 8%, southerly aspect (190°), and is considered well-drained on loamy parent material. Soils on the site have been classified as Orthic Black Chernozems (Udic Haploborall) developed on till over-lying sandstone (Dormaar and Willms 1990). Table 3.2 describes this soil. The climate is dry subhumid with a mean annual precipitation of 550 mm. Growing season (April to August, inclusive) precipitation totaled 351 and 171 mm in 1999 and 2000, respectively at the Stavely sub-station (Table 3.3). Long-term (e.g., 40-year) monthly averages for precipitation during the growing season are also provided in Table 3.3, and indicate above normal precipitation in 1999 (+23%) and below normal precipitation in 2000 (-40%).





### 3.2.2 WildFire Description

The study site was burned by wildfire on April 7, 1999 around 2 pm. The fire resulted due to an escape from small-plot burn research being conducted in one corner of the exclosure at the time. Sustained wind speeds were greater than those considered suitable for large-scale burning, approximately  $20 \text{ km h}^{-1}$ , gusting to greater velocities: average wind speed for the day was  $30.2 \text{ km h}^{-1}$  (AAFC 2000). Air temperatures averaged  $6.7^{\circ}\text{C}$  for the day with a low of  $0.9^{\circ}\text{C}$  and a high of  $13^{\circ}\text{C}$ . Average temperatures recorded at the soil surface and 10cm below the surface were  $7^{\circ}\text{C}$  and  $2^{\circ}\text{C}$ , respectively. Relative humidity in the morning was 50%, dropping to 30% at the time of the fire. Total incoming radiation was  $15,594 \text{ KJ m}^{-2}$  under slightly overcast skies. Unburned litter (coarse, largely undecayed natural mulch) fuel loads within the exclosure as measured in 1999 were  $6,372 \text{ kg ha}^{-1}$ , with a 12-year average of  $5,334 \text{ kg ha}^{-1}$  (AAFRD-Public Lands Division 1999). These fuel loads are relatively high for *Festuca-Danthonia* grasslands, which generally average 4,359 and  $3,229 \text{ kg ha}^{-1}$  for ungrazed and lightly grazed rangeland, respectively (Johnston 1961).

The fire occurred immediately following snowmelt but before the initiation of plant growth. Although only one hectare was burned, the fire was considered intense, destroying permanent fences, and inflicting considerable visible damage (e.g., pitting) to rough fescue tussocks. The exclosure fence was promptly rebuilt to exclude cattle grazing, and provided the opportunity to conduct a detailed investigation into the response of rough fescue plants following wildfire.



### 3.2.3 *Experimental Design*

Rough fescue plants (N=120) were randomly selected from within the burned and adjacent unburned areas of the exclosure for investigation following the fire. Plants were randomly selected using unsorted wooden stakes, which were marked with the type of defoliation treatment plants would be subject to. These stakes were permanently assigned to plants that met the criteria of having a diameter of approximately 15-20 cm near the base of the tussock and had a relatively uniform basal area. In September 1999, an additional 10 plants were randomly selected in each of the burned and unburned areas to act as an undefoliated check. These plants were added for qualitative comparison and were not included in the inferential statistical analysis.

The effects of subsequent defoliation intensity (represented by 5 and 15-cm clipped stubble heights) and defoliation season (May 17<sup>th</sup>, July 2<sup>nd</sup>, or September 30<sup>th</sup>), on burned and unburned plants were evaluated in a 2 x 3 x 2 factorial experiment with 10 replicates of each treatment combination. Defoliation dates represented different phenological stages of rough fescue growth. Plants defoliated in May were expected to be in active vegetative growth, the majority of which is typically completed by the end of June (Stout et al. 1981). July defoliation corresponds with the date of inflorescence development in rough fescue plants (Johnston and MacDonald 1967) and is considered a deferred grazing strategy. Fall (i.e., September) defoliated plants were dormant at the time of treatment. Unclipped control treatments were added in September of 1999 in both burned and unburned areas. All defoliation treatments were conducted during the first growing season following the April 1999 fire to evaluate the additive effects of a single defoliation event following burning. All herbage clipped in 1999 was collected to



assess dry matter (DM) removal per plant under various defoliation (i.e., grazing management) regimes.

Of the ten plants within each burn and defoliation treatment combination in 1999, two were assessed for etiolated growth during the spring of 2000. Etiolated growth provides an indication of the energy reserves available for plant growth (Raese and Decker 1966, Dovrat et al. 1972), and thus is influenced by previous management. Phytomass was removed as near as possible to the ground level on plants selected for measurement of etiolated growth. Cones were placed over these plants with soil around the bottom of the cone to completely exclude light. Etiolated plants were clipped bi-weekly commencing May 2, until growth ceased (approximately one month). Herbage of etiolated growth was oven dried and weighed.

Tiller counts were made on all plants in the fall of 1999 following completion of the various defoliation treatments. These were subsequently repeated on the 8 remaining, non-etiolated, plants in each treatment in the third week of May, second week of July, and last week of September 2000, in order to track the demographic changes in tiller numbers through time as a result of each burn by defoliation treatment combination. The number of inflorescences (e.g., seedheads) per plant was recorded in late July 1999, excluding plants that were defoliated early in July due to the interference of defoliation on seedhead production at this time. Inflorescence counts were recorded on all plants in July 2000 as well. Plant height measurements were taken at the end of the growing season in 1999 on undefoliated plants, and for all plants during the growing season in 2000 on the same dates as tiller counts were taken. Plant height was measured as the average extended length of tillers. In 2000, maximum above-ground net primary





production (ANPP) was harvested near ground level on September 30<sup>th</sup> from each rough fescue plant monitored. All herbage was oven dried and weighed.

### *3.2.4 Analysis*

All data were analyzed using ANOVA procedures (Proc GLM, Steel et al. 1997) to test for burn and defoliation effects, as well as their interactions, on ANPP production and maximum plant height in 2000 and inflorescence numbers in 1999 and 2000. P-values for the differences of the LS-means were adjusted for multiple comparisons according to Tukey's procedure. Inflorescence numbers were analyzed as percent of total tillers to adjust for unequal tiller numbers per plant. Plant ANPP levels were also combined with tiller counts and converted to tiller weights ( $\text{mg tiller}^{-1}$ ) prior to analysis. Tillers per plant and tiller phytomass data were normalized using a square root transformation to meet the conditions of normality based on the Shapiro-Wilk statistic and homogeneity of variance based on Levene's test (Proc GLM, Steel et al. 1997). Inflorescence data were also transformed using a square root transformation.

Although this study involved a single burn, variability in fuel loading and microclimatic conditions at the ground surface (e.g., microtopography, humidity, wind gusts, etc.) typically results in variable treatment exposure among individual plants, which constituted the experimental unit in this investigation. In addition, strong winds at the time of the fire enabled the backfire near the ignition source to be controlled despite the ideal conditions (fuel buildup) for wildfire. Partial containment of the fire ensured that rough fescue plants sampled on either side of the fire boundary were on the same range site.



To evaluate changes in individual plant tiller demographics, the percent change of tillers per plant was analyzed using a repeated measures multivariate analysis of variance (MANOVA). This procedure tested for the pattern of correlation between the time of sampling and main treatment effects on seasonal changes in rough fescue tiller numbers from September 1999 to May 2000, into July of 2000, and ending in September of 2000. The process of evaluating percent changes in tiller number through time also circumvented the problem that initial, pre-wildfire tiller counts were not available for use as a covariate within this study due to the initial treatment being a wildfire. Data on percent change in tillers per plant were also normalized using a square root transformation. For all analyses,  $p < 0.05$  was used to assess significance, unless otherwise noted.

### **3.3 Results and Discussion**

Observed F-ratio significance levels in the analysis of variance for the effects of spring wildfire, defoliation intensity and season, as well as their interactions, on *Festuca campestris* plant characteristics are summarized in Tables 3.4 and 3.5. Of the 140 plants selected for monitoring, all survived burning and/or defoliation throughout the two-year period except those subject to measurements of etiolated growth.

#### **3.3.1 Harvested Phytomass**

All main treatments (burn, season and intensity of defoliation) significantly affected fescue phytomass harvested (plant and tiller basis) at the time of defoliation in 1999 following spring wildfire (Table 3.4). The interaction of burn and season of



defoliation was also significant for phytomass harvested per plant, but not per tiller (Table 3.4). Additional season by clipping intensity interaction effects were evident at both the tiller and plant level (Table 3.4).

Burning reduced harvested phytomass on both a per tiller and per plant basis (Table 3.6). In general, the amount of phytomass harvested increased as defoliation shifted later into the growing season (Table 3.6), following advancing vegetative development. There were several exceptions to this pattern however, depending on whether the tiller or plant was used as the basis for evaluation. While the amount of phytomass harvested on a per plant basis increased consistently throughout the growing season, per tiller phytomass was similar between May and July defoliation periods (Table 3.6). Furthermore, examination of the burn by season interaction suggest that the similarity in tiller phytomass removal between these 2 dates was associated with unburned rather than burned fescue plants (Table 3.6).

The negligible increase in phytomass harvested from unburned plants between May and July suggests that the majority of fescue growth was complete by early to mid May. Very few new tillers are produced once stem elongation and flowering occurs in perennial grasses (Langer 1963), which would contribute little to incremental phytomass development. Unburned plants may be undergoing greater tiller development during the May to July period, which would account for the reduced per tiller phytomass by July. In contrast, phytomass harvested from burned plants consistently increased as the season progressed, likely due to slower growth during spring following the stress associated with the wildfire in early April.





As expected, a lower clipping height increased the removal of phytomass from fescue plants (Table 3.6). The significant season x intensity of defoliation effect appears to arise from an increasing difference in phytomass removal between the clipping intensity treatments as the season progressed. More intense clipping in May increased phytomass removal by as little as 57% (plant basis), while more intense clipping in September increased phytomass removal by 139% (plant basis) and 159% (tiller basis). This is likely related to differences in actual plant heights relative to the fixed clipping heights at each time of defoliation.

The reduction in phytomass harvested following burning under the clipping regimes implemented represents a net reduction in foraging opportunities for livestock and wildlife. Most important, perhaps, is the reduction in phytomass removal of burned plants relative to unburned plants appears persistent for the entire growing season following spring fire. A reduction in available phytomass coupled with the sensitivity of rough fescue to defoliation during the growing season (Willms 1991) may make grazing during the first season following spring fire impractical.

### *3.3.2 Plant Height*

Burning reduced plant height by September of 1999 (Table 3.4) from an average of 54( $\pm$ 5) cm to 25( $\pm$ 4) cm. Reduced height likely accounts for the differential phytomass removal among burned treatments, particularly when clipped at light intensities (15 cm) in September (Table 3.6). Burned plants were shorter than unburned plants, which likely influenced the variable levels of plant phytomass removed from burned and unburned plants at different dates throughout the growing season (Table 3.6).



Repeated measures analysis suggests burning decreased plant height throughout the growing season in 2000 as well (Table 3.7, Figure 3.1). Willms and Fraser (1992) postulated that shorter tillers growing more slowly could ensure plants experience a reduction in grazing pressure following a period of stress. Defoliation intensity also produced a significant response in plant height during the second growing season, particularly on unburned plants (Table 3.7, Figure 3.2). Although clipping intensity had little effect on the height of burned plants, more intense clipping reduced the year-end height of unburned plants the following year (Table 3.8), indicating that intensive defoliation is also important in causing residual changes in plant morphology.

The apparent insensitivity in the height of burned plants to clipping intensity may partly be an artifact of fixed defoliation heights. Reduced height of burned plants would reduce the susceptibility of plants to defoliation, as evidenced by the associated reduction in phytomass removal with constant clipping heights (Table 3.6). Thus, defoliation to 5 and 15 cm is likely to be more extreme for taller, unburned plants than burned plants. Clipping at fixed heights is likely to underestimate grazing impacts by selectively foraging cattle, however, particularly during spring when forage availability is low and animals readily graze close to the ground through necessity. Nevertheless, these results are similar to other studies that have shown decreases in plant height of plains rough fescue in years following either burning (e.g., Anderson and Bailey 1980, Gerling et al. 1995) or intensive defoliation (e.g., Willms and Fraser 1992) of foothills rough fescue.

Reduced height following defoliation may be a response to increased photosynthetically active radiation (PAR) at the plant crown due to the removal of senescent vegetation, or the result of increased competition among a greater number of



tillers (Willms 1988). Increases in PAR causes greater initial rates of growth for partially defoliated leaves (Willms 1988), while also increasing the rate of tillering (Langer 1963). Willms et al. (1986) found that the removal of litter alone decreases plant height, likely because of an increase in the proportion of photosynthates used for tillering. The allocation of limited plant resources (e.g., carbohydrates) to a greater number of tillers, as found in burned plants (Table 3.9), would likely result in plants with shorter stature.

### *3.3.3 Tiller Development*

Burning significantly affected year-end fescue tiller numbers in 1999 ( $p=0.088$ ) and 2000 ( $p<0.0001$ ) (Table 3.5). Season of defoliation significantly affected tiller numbers in the fall of the treatment year (Table 3.5). At the time of data collection in September 1999, the number of tillers on September defoliated plants ( $127\pm53$ ) was significantly greater than plants defoliated in July ( $98\pm38$ ), but not greater than plants defoliated in May ( $119\pm63$ ). In addition, there was a significant burning by season of defoliation interaction in 2000 (Table 3.5). Inspection of this interaction in 1999 indicated that it was significant at a p-value of 0.078.

In general, burning increased the number of tillers per plant in the year following wildfire and defoliation treatments (Table 3.9). Burning has also been shown to increase tiller numbers the year following fire in plains rough fescue (Gerling et al. 1995). Tiller mortality and recruitment is controlled by the energy and nutrient status of the plant and is reflected in changes in tiller number throughout the season (Langer 1963). A reduction in self-shading of the plant by removal of litter and above-ground biomass can stimulate





tillering (Langer 1963). Increased PAR near the crown has been shown to increase tillering in rough fescue (Willms 1988).

Season of defoliation did not produce the same effect on the number of tillers within burned and unburned plants. Defoliation in May and September produced greater tiller numbers in burned than unburned plants during 2000, while burned plants defoliated in July did not differ (Table 3.9). Thus, July defoliation appears to represent an additive stress to burning and has the impact of negating the stimulatory effect of burning on tiller development relative to either May or September defoliation. The lack of response of burned plants to spring defoliation may be related to the low amount of phytomass removed with slower growth due to the stress of the fire and fixed clipping heights (e.g., Table 3.6). During September defoliation, plants were likely senescent and thus, would have been more tolerant to the effects of defoliation.

Increased tillering by defoliation alone has been observed in a number of studies (Willms and Fraser 1992, Cuomo et al. 1998), and may include the effect of litter removal (Willms 1988). Our results, however, indicate that a single defoliation alone did not appear to affect tiller numbers, but rather depended on the associated impacts of fire. These results are similar to Willms et al. (1986) for a single defoliation. With multiple harvests, Willms (1991) found that summer defoliation (without fire) reduces rough fescue vigour including tiller numbers, making this plant vulnerable during the growing season.

Burning and defoliation intensity significantly influenced the seasonal dynamics of tiller development in rough fescue plants, as evidenced by the analysis of repeated measures (Table 3.7). Relative to unburned plants, those exposed to fire expressed a





greater relative (%) increase in tiller number the following spring (Figure 3.3) despite having similar detectable tiller numbers per plant going into winter (Table 3.9). In contrast, unburned plants had few new tillers emerge during the fall, with more tillers emerging during the following spring and early summer (Figure 3.3). Defoliation intensity also influenced tiller dynamics, with more closely defoliated plants expressing a greater percent increase in measurable tillers in the fall, and smaller changes in tillers throughout the following spring and early summer (Figure 3.4). Plants clipped to 15 cm, however, expressed a steady increase in emergent tillers through July before dropping sharply in September of 2000 (Figure 3.4).

Increases in tiller development can be attributed to accelerated spring growth due to a blackened soil surface and the removal of insulating litter, which increases soil temperatures (Savage 1980, Redmann 1993, Gerling et al. 1995). These changes also increase light penetration, thereby increasing PAR to the crown of the plant (Willms 1988) and affecting tiller demographics (Friend 1966, Rice and Parenti 1978). In contrast, unburned plants experienced a net decline in tiller numbers over winter, with maximum tiller expression during the May to July sampling intercession (Figure 3.3). A possible mechanism for increased tillering following burning is the removal of competition from apical meristems for nutrients and water, allowing a greater number of axillary meristems to initiate growth (Murphy and Briske 1992). The presence of shorter, lighter weight tillers in burned plants compared to unburned plants indicates that more tillers are competing for the same amount of nutrients and water, which were being utilized by a relatively smaller number of larger tillers before burning.



Differences in the number of tillers and their timing of development indicate the effects of spring fire extend throughout the second growing season after fire. As a result, management considerations should take these effects into account. Active tiller development during the fall following spring fire may be an important recovery mechanism for fescue plants, with adjustments in stocking rates needed to ensure conservative use and adequate carryover to maintain tiller vigour.

#### 3.3.4 Etiolated Growth

Plant vigour following disturbance can be estimated through etiolated growth, which is positively correlated with carbohydrate levels in the roots and crowns of grasses (Raese and Decker 1966, Dovrat et al. 1972). Etiolated growth samples collected in spring 2000 indicate that wildfire the previous spring had a significant effect on etiolated tiller phytomass (Table 3.5). Unburned fescue plants produced significantly more etiolated growth per tiller than did burned plants (Table 3.10), indicating that burning reduced plant carbohydrate levels one year after fire. This may be a result of new tillers being initiated in burned plants, whereas unburned plants grew new phytomass from existing tillers. Other investigators have also found reductions in etiolated tiller phytomass in species such as *Panicum virgatum*, *Andropogon gerardii*, and *Sorghastrum nutans* during the spring one season following fire (e.g., Cuomo et al. 1998).

The season of defoliation following spring fire also affected etiolated growth one year later (Table 3.5). Etiolated tiller phytomass was significantly lower for May defoliated plants relative to those defoliated in September (Table 3.10). July defoliated plants had relatively greater etiolated growth than May defoliated plants, but this



difference was considered only marginally significant ( $p=0.12$ ), likely because of the limited sample sizes employed for monitoring etiolated growth. Willms and Fraser (1992) attributed lower etiolated growth to defoliation stress causing a loss of carbohydrate reserves and reduced nutrient uptake associated with a smaller root mass. Although Johnston (1961) found rough fescue root mass to be strongly affected by defoliation, with greater root reductions due to increasing intensities of defoliation, no effect of clipping intensity for a single defoliation event was found on etiolated growth in this study.

Differences in etiolated growth suggest that plant carbohydrate levels are sensitive to stress by both fire and spring defoliation with residual effects lasting beyond the season of treatment. The lack of a burn x season of defoliation effect may be attributed to the low sample size of etiolated plants (e.g., 2 replicates per treatment), or indicative that no additive effect exists from defoliation on rough fescue carbohydrate levels following fire. Regardless, the negative impact of fire and early season defoliation indicates that management for carbohydrate reserves for long-term sustainability following these disturbances should extend for at least one full year.

### *3.3.5 Tiller and Plant Phytomass*

Burning, defoliation intensity, and their interaction significantly affected plant and tiller phytomass in measured September of 2000 (Table 3.4). Burning generally reduced plant and tiller phytomass in the second year following fire (Table 3.11, Table 3.8). The burn and clipping intensity interaction reflected an inconsistency in the impact of defoliation intensity within burn treatments. In particular, increased defoliation





intensity (to 5 cm stubble height) reduced tiller and plant phytomass in 2000, but only on unburned plants (Table 3.8), suggesting that burning counteracted the effects of defoliation intensity. An additional explanation is that below normal precipitation in 2000 may have limited the response expressed by burned plants under different intensities, particularly given the role of litter in maintaining production (Willms et al. 1986).

While there was no effect of season of defoliation alone, season did interact with burning to significantly affect plant phytomass (Table 3.4). Specifically, season of defoliation had no impact on unburned plants, while burned plants defoliated in July appeared to be the most detrimentally affected relative to those defoliated in either May or September (Table 3.11).

Burning has been shown to reduce above-ground graminoid biomass in plains rough fescue (e.g., Anderson and Bailey 1980, Redmann 1993, Gerling et al. 1995) and foothills rough fescue (Jourdonnais and Bedunah 1990) the year following burning. Antos et al. (1983) found that three years after wildfire, foothills rough fescue increased in individual plant production, but remained lower compared to fescue production from unburned areas. Recovery may be related to pre-burn fuel loads, as both sites [Antos et al. (1983) and this study] were burned by wildfire after being ungrazed and fire-free for more than twenty years.

The lack of a significant response to season of defoliation alone is contrary to the findings of Willms (1991), who found growing season defoliation to be the most detrimental to yield in subsequent years. However, these findings were only evident after multiple seasons of harvest. The results of the current study do indicate that mid season



defoliation does impose an additive stress on burned plants, as evidenced by reduced rough fescue yields. Unlike plant phytomass, tiller phytomass was more detrimentally affected by defoliation intensity than season of defoliation.

Declines in plant productivity following fire can be attributed to water stress (Redmann 1978). Savage (1980) found that drought conditions were probable following fire due to increased evaporation from the warmer, blacker surface and reduced field capacity of the soil. Even though precipitation for the 1999 growing season was higher (+23%) than the long-term average immediately following the fire (Table 3.3), modifications in the microclimate may reduce moisture availability to the plant causing water stress.

Weather conditions for the two years following wildfire may also be crucially important to the longer-term recovery of burned plants. Growing season precipitation was considerably lower in 2000, the year following fire, being 60% of the long-term average. During this time, the productivity of burned plants remained lower than unburned plants, suggesting that changes in the microclimate may have caused water stress in the burned area. May and July precipitation in 2000 was considerably below the 40-year average for these months, being 27 and 23% of the long-term amounts, respectively (Table 3.3). Thus, although insufficient recovery of defoliated plants in the first year may have influenced second year production, low precipitation at these times likely exacerbated drought-like conditions caused by fire and also affected plant recovery. Bork et al. (2000) also found a decline in graminoid production after wildfire on fescue rangeland, but recovery occurred within 2 years, in part due to highly favourable precipitation the first growing season after fire.



### 3.3.6 Inflorescence Production

Burning affected rough fescue inflorescence production in the year of treatment (Table 3.5). Inflorescence densities on burned and unburned plants were 0.07% ( $\pm 0.87$ ) and 0.38% ( $\pm 1.75$ ) of the total number of tillers on fescue plants, respectively. In contrast, both burning and season of defoliation, along with their interaction, affected inflorescence production one year later, in 2000 (Table 3.5). In general, burning decreased the proportion of reproductive tillers per plant through two years after fire relative to unburned plants (Figure 3.5). While there was no difference in inflorescence production for burned plants defoliated in different seasons, July defoliation of unburned plants reduced inflorescences relative to those defoliated in May or September (Figure 3.5). Seedhead densities from unburned plants defoliated in July were similar to those of burned plants.

The effects of burning found in this study on inflorescence production were similar to those found by Bailey and Anderson (1978), who reported either no effect or a suppression of inflorescence production within *Stipa spartea* var. *curtiseta* and *Festuca scabrella* (*hallii*) for 3 years after a spring burn. Other studies (e.g., Gerling et al. 1995, Bork et al. 2000), however, have indicated that rough fescue inflorescence production increases in the second year following fire, a finding not substantiated here. In the study by Bailey and Anderson (1978), precipitation was below average in August and September, which may have suppressed floral initiation occurring late in the summer (Johnston and MacDonald 1967). In this study, August and September precipitation in 1999 (the year of treatment) were low at 89 and 38% of the 40-year monthly averages,





respectively (Table 3.3). This suggests moisture may have limited inflorescence development. Knapp and Hulbert (1986) found that a wet year following a drought stimulates flowering. Bork et al. (2000) also reported an overall positive response of rough fescue seedhead production to high levels of precipitation, and may account for the observed differences between studies. Thus, while the potential for increased seedhead production following fire is apparent (Daubenmire 1968), it appears that adequate moisture is a prerequisite to generating this response, at least within foothills rough fescue.

The marked reduction in inflorescence production one year following July defoliation, particularly on unburned plants, suggests foothills rough fescue sexual reproduction is particularly susceptible to disruption if defoliated at that time of the growing season. Gerling et al. (1995) demonstrated a similar reduction, where burning or mowing after June 1 reduced inflorescence density one year later.

Seed set is important in rangeland that is in poor or fair condition where the number of rough fescue plants has been diminished due to over-grazing, and plants must re-establish by seed (Johnston and MacDonald 1968). High inflorescence production on rangelands in good condition, however, is not essential as plants are relatively long-lived and maintained asexually by tillering. As no mortality of rough fescue was observed in this study following fire and defoliation treatments, the existing rough fescue plants should facilitate recovery.

Nevertheless, these findings reinforce the importance of avoiding defoliation of foothills rough fescue during the late stages of active growth and inflorescence development (e.g., July) (Willms 1991), particularly if seed production is a key objective





in management. Seed production may be desirable, for instance, to facilitate the re-establishment of rough fescue following a disturbance such as fire. In contrast, the results documented in this study indicate that a single defoliation during the spring, presumably before maximum sensitivity to defoliation, does not reduce rough fescue inflorescence production in the long-term.

### **3.4 Conclusions and Management Implications**

Spring wildfire reduced the height of rough fescue plants, inflorescence production, and plant and tiller phytomass production. This effect persisted for at least two full growing seasons relative to unburned rough fescue plants. Burning also decreased the production of rough fescue phytomass harvested in the first year following fire. Burned plants were shorter, but had a greater number of tillers per plant. This resulted in individual tillers with less mass on burned plants compared with unburned plants. The influence of climatic conditions, especially precipitation, during the post-fire period also likely affected the results seen here. Following the spring wildfire, above average rainfall created favourable conditions for plant recovery, but markedly lower precipitation in the second growing season likely influenced second-year plant responses as well.

In this study, both the season of defoliation and intensity of defoliation impacted rough fescue morphology. Season of defoliation influenced the proportion of reproductive tillers and etiolated growth from fescue plants, while defoliation intensity affected plant height as well as plant and tiller phytomass. Both season and intensity of defoliation affected tiller numbers. In general, July defoliation following burning was



found to be more detrimental to fescue growth than May defoliation in terms of tiller counts and long-term inflorescence production. An exception was etiolated growth, which indicated May defoliated plants had the lowest root carbohydrate reserves one year later. Intensive defoliation reduced plant height one year later, along with plant and tiller phytomass, but these reductions were generally limited to unburned plants. These results highlight the fact that burned plants respond differently to imposed defoliation treatments relative to unburned plants. Unburned plants are generally more susceptible to intensive defoliation, particularly early in the year, as they are actively growing at that time. In contrast, burned plants regrow relatively slowly, reducing the risk of grazing damage early in the year, even at high defoliation intensities (e.g., 5 cm stubble height).

These results indicate that rangeland managers and graziers will have to make decisions on which morphological variables they believe are the most important in order to sustain burned rough fescue rangeland. In order to maximize the recovery of burned rough fescue (and all the characteristics examined), grazing would have to be deferred into the fall. However, other options may be available to land managers in order to facilitate rapid recovery of burned areas by replacing components of grasslands removed by fire. This might involve the addition of nutrients (nitrogen and sulfur) to the soil, litter to the soil surface or irrigation to avoid moisture deficits.

Although the fescue plants examined in this study appeared relatively resilient to spring grazing, the limited impact associated with May defoliation is at least partly due to the limited growth of fescue plants that had occurred by that time following the fire. Grazing in early spring following fire may be a viable option on fescue rangelands provided other forage species are available and/or fescue plants are avoided in favour of



other plants. In addition, an early season grazing strategy (e.g., skim grazing, or short grazing periods at low stocking rates) may help facilitate long-term rough fescue recovery by keeping introduced species in check, particularly if they initiate growth before or more rapidly than, slowly regrowing rough fescue plants. An increase in non-native, invasive species such as Kentucky bluegrass (*Poa pratensis* L.) following fire has been a concern of ranchers in the foothills region (B. Adams, pers. communication). Appropriate grazing following fire could limit the cover of introduced grasses, and thereby limit any competitive advantage they gain with total resting of fescue rangeland following fire. However, additional research is needed to address specific, inter-specific and animal-grazing issues before any reliable conclusions can be drawn.





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**Table 3.1 Composition of major plant species in the exclosure at Stavely, Alberta (from Willms et al. 1996).**

Species	% Composition <sup>1</sup>
Grasses and sedges	
<i>Agropyron dasytachyum</i>	1.1
<i>Agropyron subsecundum</i>	1.1
<i>Agrostis scabra</i>	0.6
<i>Bromus inermis</i>	2.6
<i>Danthonia parryi</i>	16.7
<i>Festuca campestris</i>	41.1
<i>Festuca idahoensis</i>	3.9
<i>Poa pratensis</i>	2.3
<i>Stipa comata &amp; viridula</i>	1.7
<i>Carex spp.</i>	4.6
Forbs	
<i>Achillea millefolium</i>	2.0
<i>Artemisia frigida</i>	<0.1
<i>Aster ericoides &amp; laevis</i>	5.5
<i>Galium boreale</i>	5.2
<i>Taraxacum officinale</i>	0.1
<i>Thermopsis rhombifolia</i>	0.3
Shrubs	
<i>Potentilla fruticosa</i>	1.5

<sup>1</sup> Composition is based on basal area determined by point sampling.

**Table 3.2 Pedon description of the Orthic Black Chernozemic soil within the exclosure examined at AAFC sub-station near Stavely, Alberta (AAFRD 1999).**

Horizon	Depth	Description
Ah	0-19	Black (10YR 2/1 matrix moist) and black (10YR 2/1 matrix dry); clay loam; moderate fine granular; very friable; abundant, fine, random, matrix roots; no effervescence; 16-24cm thick.
Bm	19-57	Dark brown (10YR 3/3 matrix moist); gravelly clay; weak to moderate medium subangular blocky; friable; plentiful, fine, vertical, matrix roots; no effervescence; 35-43 cm thick.
Cca	57-80	Brown (10YR 5/3 matrix moist); gravelly clay; weak to moderate fine pseudo subangular blocky; very friable; plentiful, fine, vertical, matrix roots; strong effervescence.





Table 3.3 Winter (January to March, November, December), monthly growing season, and 40-year average precipitation on the Fescue Prairie AAFC sub-station near Stavely, Alberta, from 1997 to 2000.

	Jan – Mar	April	May	June	July	August	Sept	October	Nov – Dec	Total
	----- (mm) -----									
1997	21.9	21.4	138	73.1	28	77	34.9	0.2	4.9	399.4
1998	47.5	27.9	169.6	186.9	129.7	16.2	25.3	12.5	31.9	647.5
1999	10.9	66.2*	71.6	109	53.9	50.3	15.6	8.6	12.6	398.7
2000	23	27	16.6	66.2	13.1	48.1	59.9	1.6	8	263.5
40-yr average	76.2 <sup>#</sup>	27.2 <sup>#</sup>	61.8	84.1	56.1	56.8	40.8	22.6	44.8 <sup>#</sup>	444.3 <sup>#</sup>

\*Indicates time of wildfire, April 7, 1999.

<sup>#</sup>Data from the Claresholm Meadow Creek, Alberta climate station, 1961-1990 (Environment Canada 1998).



Table 3.4 Observed F-ratio significance levels for height and phytomass changes of *Festuca campestris* plants in September of 1999 (the year of spring wildfire and defoliation treatments) and one year later in September of 2000.

Variable:	d.f.	Height (cm) plant <sup>-1</sup>		Phytomass harvested (mg) tiller <sup>-1</sup>		ANPP <sup>1</sup> (mg) tiller <sup>-1</sup>		ANPP <sup>1</sup> (g) plant <sup>-1</sup>	
		(N=20) 1999	(N=96) 2000	(N=120) 1999	(N=120) 2000	(N=96) 1999	(N=96) 2000	(N=96) 1999	(N=96) 2000
-----p-value-----									
Burn (B)	1	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Season of defoliation (S)	2	-	0.65	0.0005	<0.0001	0.89	0.30	0.05	0.05
Clipping intensity (C)	1	-	0.0003	<0.0001	<0.0001	0.02	0.18	<0.05	0.02
B x S	2		0.13	0.12	0.0008	0.15	0.01	0.24	0.68
B x C	1		0.04	0.88	0.03	0.69	0.91	0.37	
S x C	2		0.83	0.02	0.03	0.91	0.37		
B x S x C	2		0.39	0.18	0.18	0.18	0.18	0.18	0.18

<sup>1</sup>p-values are reported based on analysis performed using transformed data. Arithmetic means and standard deviations of original data are presented in tables and figures.

Table 3.5 Observed F-ratio significance levels for etiolated growth per tiller (May), percent seed heads (July) and tiller counts (September) of *Festuca campestris* plants in 1999, the year of spring wildfire and defoliation treatments, and 2000<sup>1</sup>.

Variable:	d.f.	Tillers plant <sup>-1</sup>		% Reproductive tillers plant <sup>-1</sup>		Etiolated growth (mg) tiller <sup>-1</sup>
		(N=120) 1999	(N=96) 2000	(N=60) <sup>2</sup> 1999	(N=96) 2000	
		-----p-value-----				
Burn (B)	1	0.09	<0.0001	0.01	0.01	0.01
Season of defoliation (S)	2	0.04	0.13	0.62	<0.0001	0.03
Clipping intensity (C)	1	0.19	0.45	0.52	0.97	0.66
B x S	2	0.08	0.04	0.09	0.04	0.23
B x C	1	0.81	0.34	0.40	0.70	0.94
S x C	2	0.43	0.72	-	0.27	0.38
B x S x C	2	0.59	0.14	-	0.17	0.18

<sup>1</sup>p-values are reported based on analysis performed using transformed data. Arithmetic means and standard deviations of original data are presented in tables and figures.

<sup>2</sup>Analysis of %reproductive tillers per plant is based on spring defoliated and undefoliated plants due to obvious interference of summer defoliation with inflorescence production (d.f. =1 for all variables tested).



Table 3.6 Phytomass harvested from *Festuca campestris* plants (N=120) during the first growing season following a spring wildfire and different seasons and intensities of defoliation in 1999.

Treatment <sup>1</sup>	Tiller phytomass mg tiller <sup>-1</sup>	Plant phytomass g plant <sup>-1</sup>
<b>Burn treatment</b>		
Burned	30.6 <i>a</i>	2.87 <i>a</i>
Unburned	99.1 <i>b</i>	10.91 <i>b</i>
<i>Standard error</i>	5.9	0.51
<b>Season of defoliation</b>		
May	52.8 <i>a</i>	4.7 <i>a</i>
July	52.9 <i>a</i>	6.81 <i>b</i>
September	88.8 <i>b</i>	9.16 <i>c</i>
<i>Standard error</i>	7.2	0.62
<b>Clipping Intensity</b>		
5 cm	87.5 <i>a</i>	9.16 <i>a</i>
15 cm	42.1 <i>b</i>	4.61 <i>b</i>
<i>Standard error</i>	5.9	0.51
<b>Burn x Season</b>		
Burned x May	6.4	0.38 <i>e</i>
Burned x July	23.5	2.93 <i>d</i>
Burned x Sept	61.7	5.31 <i>c</i>
-----		
Unburned x May	99.1	9.03 <i>b</i>
Unburned x July	82.4	10.7 <i>ab</i>
Unburned x Sept	115.8	13.01 <i>a</i>
<i>Standard error</i>	10.2	0.88
<b>Season x Intensity<sup>2</sup></b>		
May x 5cm	67.1 <i>bc</i>	5.74 <i>c</i>
May x 15cm	38.4 <i>c</i>	3.66 <i>d</i>
-----		
July x 5cm	67.2 <i>a</i>	8.84 <i>b</i>
July x 15cm	38.6 <i>c</i>	4.79 <i>c</i>
-----		
Sept x 5cm	128.1 <i>a</i>	12.92 <i>a</i>
Sept x 15cm	49.4 <i>bc</i>	5.4 <i>c</i>
<i>Standard error</i>	10.2	0.88

<sup>1</sup> Within a column and treatment, means followed by different letters differ significantly (p<0.05).





**Table 3.7 Multivariate analysis of variance for repeated measures of height (May – July – September 2000) and percent change in tiller numbers (September 1999 – May – July – September 2000) of *Festuca campestris* plants (N=96).**

	DF	Height (cm plant <sup>-1</sup> )	Tillers plant <sup>-1</sup> *
		-----p-value-----	
Date of measurement (D)	1	<0.0001 <sup>1</sup>	<0.0001 <sup>1</sup>
D x Burn (B)	1	<0.0001	<0.0001
D x Season of defoliation (S)	2	0.17	0.57
D x Clipping intensity (C)	1	0.01	0.05
D x B x S	2	0.28	0.27
D x B x C	1	0.10	0.57
D x S x C	2	0.23	0.6
D x B x S x C	2	0.15	0.31

\* p-values are reported based on analysis performed using transformed data. Arithmetic means and standard deviations are presented for original data in accompanying tables and figures.

<sup>1</sup> Preference was given to Pillai's Trace when differences occurred in the p-value of MANOVA tests.

**Table 3.8 Mean height and phytomass of *Festuca campestris* plants (N=96) measured in September 2000, following spring wildfire and defoliation at two intensities in 1999.**

Treatment	Plant height ---cm plant <sup>-1</sup> ---	Tiller phytomass ---mg tiller <sup>-1</sup> ---	Plant phytomass ---g plant <sup>-1</sup> ---
<b>Burned</b>			
5cm stubble height	24 a <sup>1</sup>	43.8 a	9.63 a
15cm stubble height	26 a	43.0 a	8.78 a
<b>Unburned</b>			
5cm stubble height	39 b	121.7 b	15.3 b
15cm stubble height	46 c	153.4 c	22.4 c
<i>Standard error</i>	1	0.6	1.4
Total burned	25 A <sup>2</sup>	43.4 A	9.2 A
Total unburned	43 B	137.5 B	18.8 B
<i>Standard error</i>	1	0.4	1.0

<sup>1</sup> Within a column, means followed by different lower case letters differ significantly (p<0.05).

<sup>2</sup> Grand means within columns followed by different upper case letters differ significantly (p<0.05).



**Table 3.9** Year-end (September) tiller counts of *Festuca campestris* plants in 1999 (N=120) and 2000 (N=96) after spring wildfire and defoliation on three dates in 1999.

		Defoliation Season				
Sampling Year	Treatment	May	July	Sept	All Seasons (Mean)	Undeveloped check
		----- tillers plant <sup>-1</sup> -----				
Sept 1999						
	Burned	139 <i>xy</i> <sup>1</sup>	93 <i>y</i>	142 <i>x</i>	125 <i>A</i> <sup>2</sup>	125
	Unburned	100 <i>xy</i>	103 <i>xy</i>	113 <i>xy</i>	103 <i>B</i>	92
	Standard error	-----	11	-----	7	16
Sept 2000						
	Burned	234 <i>x</i>	168 <i>xy</i>	207 <i>x</i>	203 <i>A</i>	195
	Unburned	140 <i>y</i>	140 <i>y</i>	118 <i>y</i>	132 <i>B</i>	114
	Standard error	-----	15	-----	9	26

<sup>1</sup> Within a sampling year, means followed by different lower case letters differ significantly (p<0.05).

<sup>2</sup> Within a column and sampling year, burned and unburned means followed by different upper case letters differ significantly (p<0.05).

**Table 3.10** Mean accumulated etiolated growth of *Festuca campestris* plants in May 2000 following burning and defoliation at different dates in 1999.

Variable	N	Weight ---mg tiller <sup>-1</sup> ---
<b>Burn Treatment</b>		
Burned	12	9.0 <i>A</i> <sup>1</sup>
Unburned	12	16.2 <i>B</i>
<i>Standard error</i>		1.8
<b>Season of defoliation</b>		
May	8	7.4 <i>a</i>
July	8	14.0 <i>ab</i> <sup>2</sup>
September	8	16.3 <i>b</i>
<i>Standard error</i>		2.2
Undeveloped control	4	16.3

<sup>1</sup> Within a variable, means followed by different letters differ significantly (p<0.05).

<sup>2</sup> May and July differ at p=0.12 for the season of defoliation effect.



Table 3.11 Phytomass produced for burned and unburned *Festuca campestris* plants (N=96) in September 2000, following defoliation in 1999, during either May July or September.

Variable:	ANPP
	----g·plant <sup>-1</sup> ----
Burned x May	11.48 a <sup>1</sup>
Burned x July	6.51 b
Burned x Sept	9.63 ab
Unburned x May	19.48 c
Unburned x July	20.33 c
Unburned x Sept	16.69 c
Standard error	1.74
Burned x undefoliated check	9.66
Unburned x undefoliated check	20.14

<sup>1</sup> Means followed by different letters differ significantly (p<0.05).

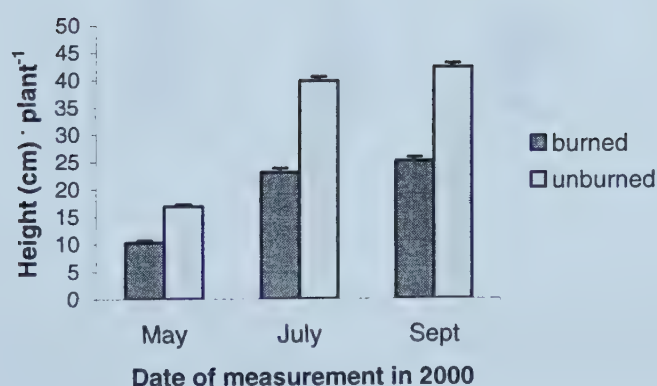


Figure 3.1 Mean height (+SE) over three seasons in 2000 of burned and unburned *Festuca campestris* plants (N=96).



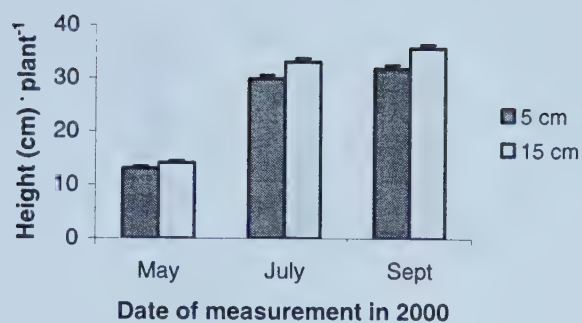


Figure 3.2 Mean height (+SE) over three seasons in 2000 of *Festuca campestris* plants (N=96) receiving intense (5cm-stubble height) and light (15cm-stubble height) defoliation treatments in 1999.

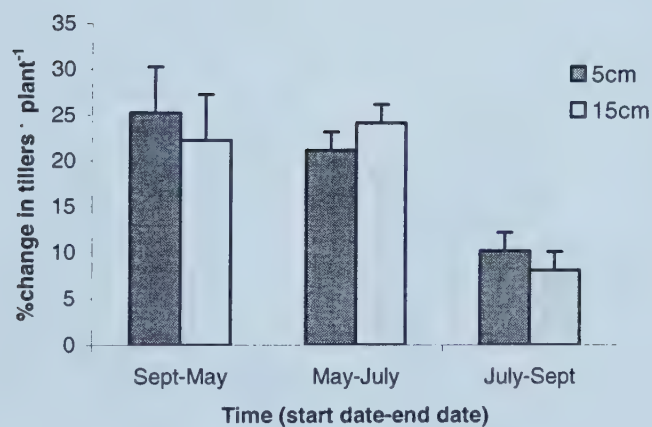
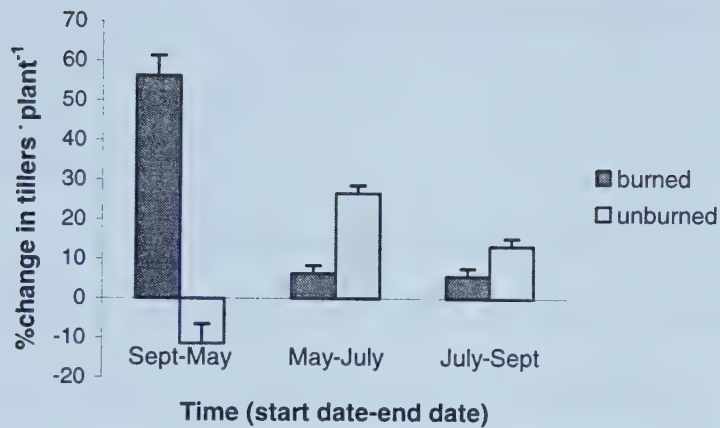


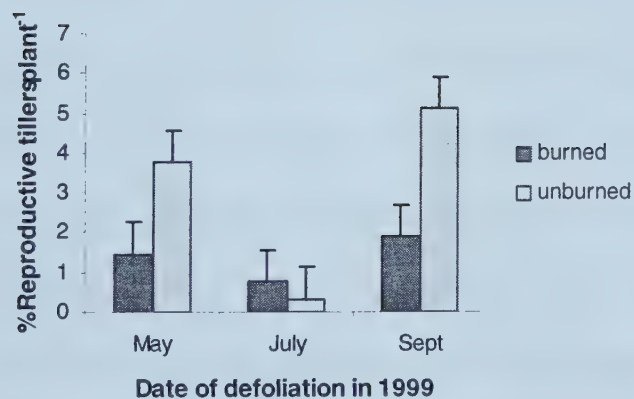
Figure 3.3 Percent change in tiller number (+SE) of *Festuca campestris* plants (N=96) between Sept 1999 and Sept 2000 during each of three periods following clipping to 5cm- and 15cm-stubble heights in 1999.







**Figure 3.4** Seasonal percent change in tiller numbers (+SE) of burned and unburned *Festuca campestris* plants (N=96) between Sept 1999 and Sept 2000, during each of three periods.



**Figure 3.5** Relative proportion of reproductive tillers (+SE) of burned and unburned *Festuca campestris* plants (N=96) in July 2000, following fire and defoliation at different dates in 1999.



## 4 Response of *Festuca campestris* to Heat Injury

### 4.1 Introduction

Fire within natural landscapes is an important factor in maintaining diverse and productive ecosystems (Vogl 1974). The Fescue Prairie of southwestern Alberta is a fire maintained ecosystem with a historical fire frequency of 5-10 years (Wright and Bailey 1982). *Festuca campestris* Rydb. is the dominant climax species of grasslands throughout the region (Moss and Campbell 1947, Looman 1969) and provides an economical and practical source of fall and winter grazing for commercial ranches (Willms et al. 1993).

During fire, temperatures near the soil surface have been found to vary greatly in grasslands. The maximum temperature and duration of elevated temperature is influenced by a variety of factors, including fuel loads, fuel moisture content and weather conditions during fire. Average temperatures ranging from 102°C to 388°C have been reported for fires in the Great Plains (Stinson and Wright 1969), the Aspen Parkland (Bailey and Anderson 1980, Archibold et al. 1998), and other grassland systems (Bentley and Fenner 1958, Britton and Wright 1971). Higher temperatures have been associated with greater fuel biomass in grasslands (Stinson and Wright 1969, Bailey and Anderson 1980, McDaniel et al. 1997, Archibold et al. 1998, Morgan 1999). The total amount of heat experienced by a plant during burning generally increases with greater fuel loads (Johnston and Woodard 1985). This is especially true when fuels are readily available, as fire will not burn without dry fuel to ignite and facilitate flame spread. In grasslands, a fuel load of 1000 kg·ha<sup>-1</sup> uniformly and continuously distributed has been suggested as



the minimum required to propagate fire (Bailey 1986). In *Themeda triandra* dominated tussock grasslands of southeast Australia, Morgan (1999) found that the duration of temperature increase to greater than 100°C at the soil surface was strongly correlated to fuel load. Greater fire temperature and associated exposure time on *Bouteloua gracilis* rangeland in Texas are strongly correlated with increasing air temperature and total fuel biomass (McDaniel et al. 1997). Greater air temperature and fine fuel cover in turn, positively influences shrub and grass mortality.

Accumulations of loosely packed litter and high winds created by fire generally result in greater air temperatures at the soil-air interface (Wright and Bailey 1982). Greater wind speeds may also increase the rate of fire spread, thereby increasing fire intensity (i.e., Byram 1959, Alexander 1982) but decreasing the duration of elevated temperature experienced by the plant along with subsequent injury (McDaniel et al. 1997, Morgan 1999). In forest ecosystems, fire intensity, as determined by the fire behavior models of Byram (1959), Rothermel (1972) and Van Wagner (1973), are more strongly influenced by weather than fuel (Fryer and Johnson 1988, Bessie and Johnson 1995). Measurements of fire intensity alone, however, do not necessarily reflect the total amount of heat experienced by a plant and therefore, the likelihood of plant damage. Fire severity, as measured by damage inflicted on vegetation or depth of burn into the organic layer, is often a more appropriate ecological descriptor of fire impacts on the landscape (Feller 1998). Thus, the duration of elevated temperature is important when soil is burning as plant roots may be killed or consumed by fire.

Plant tissue is susceptible to injury from combustion gases produced by fire. Exposure can be lethal provided a sufficiently high temperature is maintained for a





minimum period of time (Hare 1961, Yarwood 1961, Wright 1970). A temperature of 60°C has been given as the lowest temperature required to kill plant tissue at a fixed period of 10 minutes (Wright and Bailey 1982). Although exposure of plant tissue to a maximum temperature is important during fire events, the duration of elevated temperatures may be equally important. Wright (1970) found a range of maximum temperature and exposure time combinations were equally capable of killing growing points of *Sitanion hystrix* (Nutt.) J.G. Smith and *Stipa comata* Trin. & Rupr. Similarly, interspecific differences may also exist with respect to fire tolerance. In the examination of four grass species to lethal temperatures, Jameson (1961) reported that culm mortality varied between 60° and 75°C. The minimum thermal stress required to cause plant mortality varied among species, as did the method used to cause temperature stress and the type of vegetative material exposed to heat.

Effects of the time-temperature relationship on coniferous species have been extensively examined. Lorenz (1939) reported lethal temperatures ranging from 57° to 59°C for 30 minutes and 65° to 69°C for one minute when heat was applied to the cortical parenchyma of white pine (*Pinus strobes* L.). Kayll (1963) reported lethal time-temperature dynamics of 60°C for 2-4 minutes and 65°C for less than two minutes for Scots pine seedlings (*Pinus sylvestris* L.). The needles of northern pine species, however, have been found to vary in their response, withstanding 50°C for 2 hours (Shirley 1963) or 63°C for 1 minute, while a temperature of 52°C sustained for 24 minutes caused death (Nelson 1952).

Wright and Bailey (1982) attributed variation in death of plant tissue to moisture content of the plant. Wright (1970) found that the exposure time needed to kill plant



tissue at 60°C varied from 2 to 60 minutes depending on moisture content. In their examination of coniferous species, Brown and Davis (1973) found that many variables influence plant susceptibility to heat flux, such as the initial temperature of vegetation, size and morphology of the portion of the plant exposed to heat, growth habit and season of exposure. For example, the roots of coniferous trees are more susceptible to damage due to a thinner epidermal covering than the trunk or branches (Kayll 1968). Many attributes of plant morphology and phenology therefore influence how a plant will respond to elevated temperatures and the period of time it is exposed.

Although *F. campestris* historically evolved under the influence of fire (Wright and Bailey 1982), its susceptibility to heat injury may be enhanced by the location of meristems and perenating buds above the soil surface due to its strongly tufted growth habit (Pavlick and Looman 1981). The potential for injury or mortality of *F. campestris* plants may also increase as fire continues to be suppressed on the landscape. Given the correlation of fuel load to fire temperature, a prolonged absence of fire accompanied by differential grazing pressure by selectively foraging livestock may allow fuel to accumulate on rangeland and create conditions that impose injurious temperatures on plants when fire eventually occurs.

Wildfire was largely suppressed on the landscape following settlement of the Fescue Prairie. More recently, however, there has been a noticeable increase in the number of wildfires impacting rangelands in the region. For example, from January of 1997 through August of 2000 a minimum of 8 wildfires occurred affecting nearly 33,500 ha, with at least 5 of these greater than 400 ha (B. Adams, personal communication, as cited in Bork et al. 2000). In the Fescue Prairie, smoldering of fine fuels near the plant



tussock at the soil surface during fire has been observed to extend the time plant tissue is exposed to heat stress (B. Adams, personal communication). The occurrence of elevated temperatures within and around the plant as a result of smoldering may be strongly influenced by the age of the tussock, fuel distribution due to prevailing winds, as well as wind conditions during fire. By quantifying time-temperature relationships with *F. campestris* tiller injury, land managers may be better able to relate this information to management activities that affect rates of fuel accumulation and reduce the risk of mortality or damage to *F. campestris* stands.

It has been well documented that *F. campestris* responds negatively to defoliation by grazing or clipping during the growing season (e.g., Looman 1969, Willms 1988, Willms 1991, Willms and Fraser 1992). The stress imposed by repeated removal of actively growing vegetative tissue causes reduced root mass, smaller bunch size, lower yields and possible mortality of *F. campestris* plants in subsequent years (McLean and Wikeem 1985, Willms 1991, Willms and Fraser 1992). It has been postulated that July is a crucial period for *F. campestris* development and that defoliation at this time may be detrimental, likely due to carbohydrate demands of inflorescence production or vegetative growth before carbohydrates are stored (McLean and Wikeem 1985, Willms 1991). Due to the susceptibility of *F. campestris* plants during the growing period (normally, active growth takes place from April to August), defoliation following temperature stress may have an additive negative impact on the long-term survivability of these plants.

In an attempt to determine the specific survival and growth response of *F. campestris* to a range of temperatures and associated exposure times, as well as





defoliation following temperature stress, several laboratory studies were implemented to address the following specific objectives:

1. Evaluate the effects of temperature, exposure time, and their interactions, on the survival and leaf extension of individual *F. campestris* tillers.
2. Evaluate the combined effects of temperature and subsequent defoliation on the number of tillers, tiller survival, and phytomass of *F. campestris* plants.

## 4.2 Materials and Methods

### 4.2.1 Experimental Approach

Dormant foothills *F. campestris* plants (n=4) were removed with a portion of their roots, approximately 6 inches, and soil in December 1998 from an ungrazed exclosure on native *Festuca – Danthonia* grassland. Plants were considered to be in excellent condition at the time of removal. The exclosure was located on the Agriculture & Agri-Food Canada research substation west of Staveland in southwestern Alberta. The *F. campestris* plants were stored in the dark at -10°C until treatments were applied.

*F. campestris* plants were thawed to enable individual tillers to be separated from the tussock. Tillers were trimmed to a uniform length of 7cm above the crown. Most of the root mass was removed from tillers, but without exposing the root-culm interface so as to not cause damage to the sheath. Tillers from all *F. campestris* plants collected in the field were then combined, from which a random sample of 280 tillers was taken to provide 10 replicates for each of 28 treatments (N=280) within 2 experiments. Two separate temperature experiments were then conducted.





Many methods have been used to determine the susceptibility of plant tissue to heat stress, which may contribute to the wide variation in plant response observed and reported (Brown and Davis 1973). Shirley (1936) found that for conifer seedlings, killing temperatures were higher in air than water, and higher in dry air than moist. Immersing plant material in heated water prevents heat dissipation, whereas heated air applied to a restricted portion of the material does not (Kyall 1963). Moisture is generally available from thermal degradation and combustion of fuel because hydrogen in fuels is mostly released as water (Pyne 1996). Consequently, moist heat is thought to simulate wildfire conditions more closely than dry heat (Martin et al. 1975). Estimates of heat tolerance determined using heated air in the absence of moisture might over-estimate lethal temperatures for plant material in the soil or near the soil surface during fire.

As a result, temperatures were varied using a hot water bath, with treated tillers submersed into the bath for various lengths of time. This form of treatment has been used in other studies (e.g. Shirley 1936, Kayll 1963) and has the added benefit of ensuring rapid, uniform transfer of heat to individual tillers. In this investigation, tiller heating (e.g., heat flux) provide a measure of the susceptibility of tillers to heat stress, which is assumed to reflect the effects of exposure to fire, at least in part.

In the initial experiment, hot water treatments were applied to randomly selected *F. campestris* tillers at temperatures of 40, 50, and 60°C, for a duration of either 1, 2, 5, or 10-minutes (Experiment 1). Ten tillers were treated in each temperature – exposure time combination. One group of ten tillers was not subjected to a water bath to act as a control. However, an additional temperature treatment of 23°C was conducted at a later date to act as a comparative baseline to other temperatures for a given time period of



exposure. This treatment was conducted to account for any effect submersion in water may have had on tillers.

From observations made in the first study, it was determined that another trial be conducted (Experiment 2), this time using a narrower range of temperatures, closer to critical temperatures (50, 55, and 60°C) and much shorter exposure times (4, 8, 16, and 32 seconds). In addition to temperature and time treatments, ten tillers were randomly selected and not treated to a water bath to ensure no changes had taken place in the *F. campestris* plants between experiments that would cause tillers to respond differently, even though plants were kept in a state of dormancy in the interim.

All temperature trials were conducted in the laboratory using a hot plate to heat a 1-litre beaker of distilled water (Figure 4.1). Water temperature was monitored throughout each experiment and water was constantly stirred to maintain a uniform temperature. Water temperature was always allowed to equilibrate at the necessary temperature before treatments were imposed. *F. campestris* tillers were then submersed in groups of 5, loosely held below the surface of the water, at the appropriate temperature and time. Submersion of tillers resulted in negligible changes in observed water temperature.

To assess the biological impact of a combination of heat stress from a known temperature and subsequent defoliation on *F. campestris* plants, a third laboratory experiment was conducted. In March of 2000, twenty dormant foothills *F. campestris* plants were removed with the sod intact from native Fescue Prairie. The plants were removed from Field A at the Agriculture & Agri-Food Research Substation near Stavelly, Alberta. In the previous year (1999), only wild elk herds grazed the field during summer,



with cow/calf pairs grazing from September 15 to October 15 at moderate stocking rates. Prior to 1999, the pasture had not been grazed by cattle for three years and was considered to be in excellent range condition.

Plants extracted in March were stored at -5°C to keep them in a state of dormancy until trials were initiated. Treatments were conducted over a 3-day period beginning April 6, 2000. In preparation for treatment, all plants were trimmed to a stubble height of 3 cm above the mulch layer and the roots were trimmed to 6 cm below the mulch layer. Each of the 20 plants was subsequently cut into quarters, based on a visual estimation for an equal number of tillers per quarter. Tillers per quarter were then counted. The quarters were labeled so that each plant could be subjected to the same temperature treatment. Within a plant, quarters would be subject to 4 different rest periods prior to defoliation following heat treatment. Thus, defoliation treatments were “blocked” on plant to negate genetic influences. All plant quarters were stored in the dark at 10°C and treated two days later. During this time, approximately 1 cm of vegetative growth occurred.

Forty quarters from ten randomly selected plants were individually submersed upside down, to 1 cm into the soil surface, into heated water for 5 minutes at 40°C. Another 40 quarters were treated for 5 minutes at 60°C. The water bath apparatus used for treatment of *F. campestris* tillers was also used for plant quarters. Heated water in the bath was stirred to ensure uniform heating.

Following treatment, plants quarters were potted in soil and grown out in a greenhouse at 20 ±3°C for 14 weeks. From each “plant”, three plant quarters were randomly selected for defoliation after one of three different rest periods, while the fourth





remained undefoliated until the end of the monitoring period. Defoliation treatments occurred at either 2, 4, or 8 weeks following heat treatment. All defoliation treatments were 2-3 cm above the height of the original stubble (3 cm), leaving 5-6 cm of culm above the soil surface.

#### 4.2.2 *Measurements and Survival*

Following treatment in Experiments 1 and 2, *F. campestris* tillers were individually labeled by treatment and replicate to track individual tiller responses. All tillers were placed within moist paper towels on a vermiculite bed. Tillers were kept in the dark in a greenhouse at  $20 \pm 3^\circ\text{C}$ , and not allowed to dry out for the duration of the monitoring period.

Leaf elongation (mm) of *F. campestris* tillers was measured at the end of three days following treatment. Measurement was discontinued at this point as tiller growth had generally slowed and factors other than response to initial heat treatment may begin to determine growth, such as tiller size and inherent variability in tiller vigour (e.g., stored carbohydrates or disease/pathogens). Tillers that exhibited no growth during this period of time were considered dead.

In the third experiment, measurements of tiller number, average plant height and phytomass removed were made at each defoliation period (e.g., 2, 4, and 8 weeks) for each potted *F. campestris* plant quarter. At the end of the 14-week monitoring period, the final tiller number, height, and phytomass was also determined for each plant quarter.



### 4.2.3 Analysis

Measurements of leaf elongation per tiller (Experiment 1 and 2) and plant phytomass (Experiment 3) at the end of the monitoring period were normalized using a square root transformation to meet the conditions of normality and homoscedasticity based on the Shapiro-Wilk statistic. ANOVA (Proc GLM, Steel et al. 1997) was used to analyze the leaf elongation and *F. campestris* tiller survival data for temperature and time of exposure, as well as their interactions. P-values for the differences of the LS-means were adjusted for multiple comparisons according to Tukey's procedure. Polynomial contrasts (Proc GLM, Steel et al. 1997) were used to determine the nature and significance of any linear, quadratic or cubic trends in the data.

Plant height and phytomass for potted *F. campestris* plant quarters at the end of the monitoring period were analyzed using ANOVA (Proc GLM, Steel et al. 1997). ANCOVA (Proc GLM, Steel et al. 1997) was used to analyze tiller number per plant quarter at the end of the monitoring period using pre-treatment tiller numbers as the covariate.

## 4.3 Results and Discussion

### 4.3.1 Tiller Mortality

Tiller mortality at temperatures below 60°C (e.g., 55°C and lower) in both trials was limited, with only 7 of 80 tillers at 50°C and 4 of 40 at 55°C failing to show any growth following treatment, regardless of exposure time (data not shown). However, at a temperature of 60°C mortality occurred and increased with longer periods of exposure,



reaching 100% with 2 minutes or longer heating (Figure 4.2). From our findings, it appears *F. campestris* is less tolerant to heat stress than other cool (e.g., *Stipa comata*) and warm season perennial grasses (e.g., *Bouteloua curtipendula*, *B. eriopoda*, *B. gracilis*, *Hilaria jamesii*, and *Sitanion hystrix*) (Jameson 1961, Wright 1970). Wright (1970) found that a duration of 55 min was required to kill *S. comata* tillers at 60°C, although the required exposure time to cause mortality dropped to 3.4 min when the temperature was raised an additional 10°C. Decreased heat stress tolerance in *F. campestris* may be due to its historical adaptation to more mesic conditions compared to the Short Grass Prairie and semi-desert communities in which the other species occur.

#### 4.3.2 Tiller Leaf Growth

Most studies determine the threshold at which temperature-time relationships cause mortality in plant tissue. In this study, tiller response to temperature-time relationships was examined as a function of mortality as well as injury, as evidenced by a reduction in tiller growth.

Analysis of trends within the data indicated tiller growth varied linearly and quadratically with temperature in both trials (Tables 4.1 and 4.2). Overall, increasing temperatures resulted in reduced tiller growth. In both experiments, however, growth also exhibited a quadratic trend and increased at a moderate heat stress of 40°C for extended exposure times (Experiment 1 - Figure 4.3) and 55°C for short times (Experiment 2 - Figure 4.5), before declining at greater temperatures.

In both experiments, the effect of exposure time alone was not significant, but did interact significantly with temperature to affect tiller growth (Tables 4.1 and 4.2). These results are depicted in Figure 4.4 and 4.6 for the first and second experiments,





respectively. An initial point at zero-time was added to the graph of Experiment 1 for comparison, but was not included in the trend analysis (Figure 4.4). This zero-time treatment was comprised of tillers not subject to any water bath treatment, but measured for tiller growth.

Significant linear trends within exposure time were found within the 50° and 60°C temperature treatments in Experiment 1 (Table 4.1), with tiller growth responding negatively to increasing exposure time. With increasing exposure time at temperatures of 23° and 40°C, there was a positive, but somewhat weak ( $0.05 < p < 0.10$ ) correlation for tiller growth (Figure 4.4). One additional quadratic effect was observed at 50°C, at which there appeared to be an initial stimulatory effect of temperature on tiller growth at an exposure time of 1 min before declining in growth with longer exposure (Table 4.1; Figure 4.4). In addition, although tiller growth initially dropped rapidly with increasing exposure at 50°C, 5 or 10 min of heating had relatively little incremental effect (Figure 4.4). The negative trend on tiller growth at 60°C in the first experiment (Table 4.1) may be inconsequential, as it coincides with severe mortality of tillers at exposure times greater than 1 min (Figure 4.2).

After determining that 50° and 60°C were critical temperatures causing a reduction in growth or mortality of *F. campestris* tillers, the second experiment was conducted using a narrower range of exposure times and temperatures. In this experiment, growth varied linearly with exposure time (Table 4.2). This significant response was largely driven by the strength of the negative linear trend associated with increasing duration of heat exposure at 60°C, as there was no significant trend for temperature within the 50° and 55°C treatments (Table 4.2). In other words, the exposure





threshold for injury to tillers that results in decreased growth appears be limited to 60°C and occur between 16 and 32 sec of exposure (Figure 4.6).

*F. campestris* tillers appear capable of withstanding a temperature of 60°C for short time periods (e.g., 16 sec or less) without experiencing a reduction in growth (Figure 4.6). This implies that during a fire, weather and existing fuel conditions that are likely to result in greater and more sustained temperatures near or above 60°C increases the risk of harming *F. campestris* plant communities. As weather conditions can only be predicted for prescribed burns and are variable in wildfire events, the only option for preventing plant community damage with fire is likely through the manipulation of fuels.

#### 4.3.3 *Festuca campestris* Plant Tiller Response

Plant mortality was minimal following the heat and defoliation treatments. All plants survived exposure to a heated water treatment of 40°C and subsequent defoliation. From one *F. campestris* plant treated at 60°C, three of the quarters died immediately following heat treatment and the fourth quarter died after defoliation at 4 weeks, suggesting this plant may have been in a weakened state prior to testing or genetically more susceptible to heat stress. One other plant quarter died after being defoliated at 8 weeks following the 60°C heat treatment.

Temperature significantly affected the final plant tiller number and the average height of tillers per plant (Table 4.3). Increasing the temperature of heated water from 40 to 60°C reduced the number of tillers and plant height (Table 4.4). Relative to pre-treatment tiller counts ( $x_{40^{\circ}\text{C}} = 34 \pm 17$  and  $x_{60^{\circ}\text{C}} = 49 \pm 16$  tillers per plant), tillering appeared to be stimulated at 40°C (+44%), but was negatively affected by the 60°C



treatment (-65%) (Figure 4.7). The increase in tiller number at the lower temperature may be a physiological response of plants to factors such as increased carbohydrate mobilization or enzyme activity. However, the lack of a complete control (e.g., plants that were not subject to any temperature treatment) rules out confirmation of this. Notably, the increase in tiller numbers on plants burned by wildfire in the field study (Chapter 3) suggests that those plant were exposed to temperatures more similar to the 40°C plants examined here.

Tillers tended to remain loosely grouped within the plant following heat treatment and did not form tightly packed bunches, as did *F. campestris* plants burned in the field (Chapter 3). Laboratory procedures used here ensured that uniform heating occurred, resulting in more equal heat treatment among tillers. In the field study, tillers near the center and especially windward side of burned plants received some amount of protection from heat as smoldering preferentially occurred around the perimeter of the leeward side of the tussock after passage of the fire front. It is also possible that the melting and hardening of silica particles within *F. campestris* tussocks during fire offered some protection from heat.

Timing of defoliation also significantly affected tiller number per plant, but not plant height (Table 4.3). As recovery time lengthened following heat treatment and prior to defoliation, final tiller numbers per plant were greatly reduced (Table 4.5). Only plants undefoliated (e.g., rested from defoliation) during the entire 14-week monitoring period experienced an increase in tiller number relative to the pre-treatment tiller data (Table 4.5).



Contrary to expectations, no temperature by time of defoliation treatment interactions were evident on any morphological parameters, suggesting that defoliation imposed no additive stress on the 60°C heat treatment. This was unexpected given the earlier results indicating *F. campestris*' increased susceptibility to temperatures of 60°C over 40°C. These results may also be constrained by the high variability within the data, particularly tiller numbers (Table 4.4). Figure 4.7 was added to demonstrate the dynamics of tiller appearance and disappearance during the monitoring period. Tiller numbers stayed relatively constant during the monitoring period after an initial increase in tillers for plants subject to a 40°C heat treatment and a decline in tillers for plants subject to a 60°C heat treatment. The decline in tiller numbers for plants defoliated 8 weeks after heat treatment clearly occurred after the defoliation event.

The mechanism for the increased susceptibility of plants to defoliation at 8 weeks is unknown, but may be linked to the amount of growth prior to defoliation. Later defoliation times (e.g., 8 weeks) would remove more phytomass, which may result in greater physiological stress and subsequent mortality of *F. campestris* tillers.

Carbohydrate reserves may also become greatly reduced as grasses near the completion of vegetative growth prior to seed formation (Smith 1972). Plants defoliated at 8 weeks, which corresponded to the greatest reduction in tillers, were given 6 weeks to recover prior to final monitoring. Given time, these plants may have recovered relative to plants defoliated earlier in the monitoring period, which were given as long as 12 weeks to recover. Despite this, there was no visual indication that plants defoliated at 8 weeks were initiating new tillers at the end of the monitoring period. Interestingly, the negative impacts of defoliation on plants in the greenhouse at 8 weeks correspond to our findings





in the field study (Chapter 3), where plants that were defoliated 12 weeks following wildfire experienced a greater reduction in tillers relative to earlier defoliation. Plant growth is generally accelerated in greenhouses due to ideal growing conditions and therefore, these plants were likely to have been in a similar phenological stage as those in the field.

#### 4.3.4 *Festuca campestris* Plant ANPP Response

Temperature and timing of defoliation following heat treatment significantly affected the standing crop harvested from *F. campestris* plants at the end of the monitoring period (Table 4.3). In contrast, total accumulated phytomass of *F. campestris* plants was significantly affected by temperature, but not timing of defoliation following heat treatment (Table 4.3). Increases in the temperature of heat treatment from 40 to 60°C decreased final standing crop and accumulated phytomass by more than 50% (Table 4.4). As plant height was not significantly affected by defoliation after varying rest periods, changes in tiller number likely accounted for differences in plant phytomass. A visible decline in accumulated tiller phytomass associated with longer rest periods between heat stress and defoliation was detected (Table 4.5), but was not significant (Table 4.4).

Although accumulated plant phytomass was not affected by the defoliation regimes implemented in this study, morphological changes in plant tiller number may be indicative of changes in plant vigour and phytomass production in subsequent years. Furthermore, it should be noted that this study examined the impacts of a single defoliation treatment only. Repeated defoliation of regrowing plants is more likely to



negatively impact future yield responses. In a study of repeated defoliation effects on *F. campestris*, Willms (1991) found that a moderate cutting frequency (e.g., 2 or 4 defoliations during the growing season) was highly detrimental to plant yield. However, it was also found that there was no immediate effect on yield in the year of treatment, with differences first observed in subsequent years, suggesting that at least 2 years of monitoring may be needed to detect changes in plant response. Our findings indicate that defoliation of *F. campestris* had the greatest impact on plant tiller number when plants are given an opportunity to regrow photosynthetic material prior to defoliation. This may correspond to future losses in forage yield.

#### 4.4 Conclusion

The response of *F. campestris* to temperature has been studied mostly within the context of the normal range of climatic conditions experienced by the plant in the absence of fire (Willms 1988, King et al. 1995). In contrast, the response of *F. campestris* following exposure to severe temperature stress is relatively unknown. The results of this research indicate that a temperature of 60°C near growing points appears to be the threshold for causing reductions in growth or mortality of *F. campestris*. *F. campestris* tillers appear capable of withstanding temperatures of 60°C for a very short time (e.g., 16 sec or less), but experience a reduction in growth at exposure times of 32 sec or more and mortality at 2 min or greater. The duration of elevated temperature is also important in causing injury to *F. campestris*, as a temperature of 50°C maintained for 5 min or greater produced a similar response to higher temperatures (e.g., 60°C) for shorter times. *F. campestris* may also experience some benefits as a result of slightly elevated



temperatures. Stimulation of growth was evident at higher temperatures (50°C) for a short exposure time (e.g., 1 min), and at more moderate temperatures (40°C) for longer exposure times.

Understanding the role of temperature - exposure time relationships on the injury or mortality of dormant tillers is important, as this information can be used to interpret prescribed or wildfire effects on *F. campestris* plants. If the goal of land managers is to maintain or enhance this species within native grasslands, then steps may be taken to avoid conditions that will cause the duration of elevated temperatures to be above that of the threshold documented in this study. Fire temperature is influenced by total available fuel (McDaniel 1997) and the duration of elevated temperature increases with greater fuel load (Morgan 1999). However, a short exposure to elevated temperatures is unlikely to occur in grassland fires, as there is generally some smoldering of fuels after the passage of the flame front.

Results found here also indicate that *F. campestris* tiller survival and growth may be further jeopardized by defoliation after heat stress. In particular, defoliation well after plants have initiated growth (e.g., 8 weeks) appears to have the most detrimental effect. Decreased plant vigour as evidenced by lower tiller numbers reinforces the notion that *F. campestris* is sensitive to defoliation during active regrowth.

Future research should be conducted to determine at what point fuel loads and their distribution in *F. campestris* grassland become capable of causing sustained temperatures in excess of the thresholds identified here. To avoid injury to *F. campestris* plants in the event of wildfire, managers may manipulate fuel loads and fuel properties through grazing alone or in conjunction with periodic prescribed fire.





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**Table 4.1 Analysis of linear, quadratic and cubic trends within the tiller growth data for a series of contrasts in Experiment 1.**

Contrast	DF	Mean Square	F Value <sup>1</sup>
Lin time	1	0.068	0.08
Quad time	1	3.071	3.73
Cubic time	1	0.04	0.05
Lin temp	1	80.013	97.18**
Quad temp	1	104.517	126.95**
Cubic temp	1	0.777	0.94
Lin time x temp	3	4.89	5.94**
Quad time x temp	3	2.81	3.41*
Lin in 23°C	1	3.182	3.87
Lin in 40°C	1	3.141	3.81
Lin in 50°C	1	5.155	6.26*
Lin in 60°C	1	3.26	3.96*
Quad in 23°C	1	0.015	0.02
Quad in 40°C	1	0.704	0.85
Quad in 50°C	1	8.246	10.02**
Quad in 60°C	1	2.537	3.08

<sup>1</sup>\*, \*\* Indicates observed F value ratio is significant at  $p < 0.05$  and  $p < 0.01$ , respectively.

**Table 4.2 Analysis of linear, quadratic and cubic trends within the tiller growth data for a series of contrasts in Experiment 2.**

Contrast	DF	Mean Square	F Value <sup>1</sup>
Lin time	1	13.0883	5.18*
Quad time	1	0.0628	0.02
Cubic time	1	8.4570	3.35
Lin temp	1	19.3612	7.67**
Quad temp	1	12.0477	4.77*
Lin time x temp	2	10.593	4.19*
Lin in 50°C	1	4.2248	1.67
Lin in 55°C	1	1.3206	0.52
Lin in 60°C	1	28.7288	11.38**

<sup>1</sup>\*, \*\* Indicates observed F value ratio is significant at  $p < 0.05$  and  $p < 0.01$ , respectively.



**Table 4.3 Observed F-ratio significance levels for tiller number, height, plant and tiller phytomass of *Festuca campestris* plants at the end of the 14-week monitoring period.**

Variable	DF	Tillers · plant <sup>-1</sup>	Height	Standing crop · plant <sup>-1</sup>	Accumulated phytomass (g) · plant <sup>-1</sup>	Weight (mg) · tiller <sup>-1</sup>
Temperature	1	<0.01	<0.01	<0.01	<0.01	0.49
Time of defoliation	3	<0.01	0.14	<0.01	0.56	0.07
Temp. x Time of defoliation	3	0.50	0.99	0.25	0.82	0.95

**Table 4. 4 Number of tillers, mean plant height, standing crop (at the end of the monitoring period) and accumulated phytomass of *Festuca campestris* plants 14 weeks following heat treatment.**

Temperature	Tillers · plant <sup>-1</sup>	Height (cm)	Weight (mg) · tiller <sup>-1</sup>	End phytomass (g) · plant <sup>-1</sup>	Accumulated phytomass (g) · plant <sup>-1</sup>
40°C	49 <i>a</i>	25 <i>a</i>	42.9	1.85 <i>a</i>	2.47 <i>a</i>
60°C	17 <i>b</i>	18 <i>b</i>	47.2	0.80 <i>b</i>	1.08 <i>b</i>
<i>Standard error</i>	4	1	4.4	0.16	0.18

<sup>1</sup> Means within columns followed by different letters differ significantly (p<0.05).

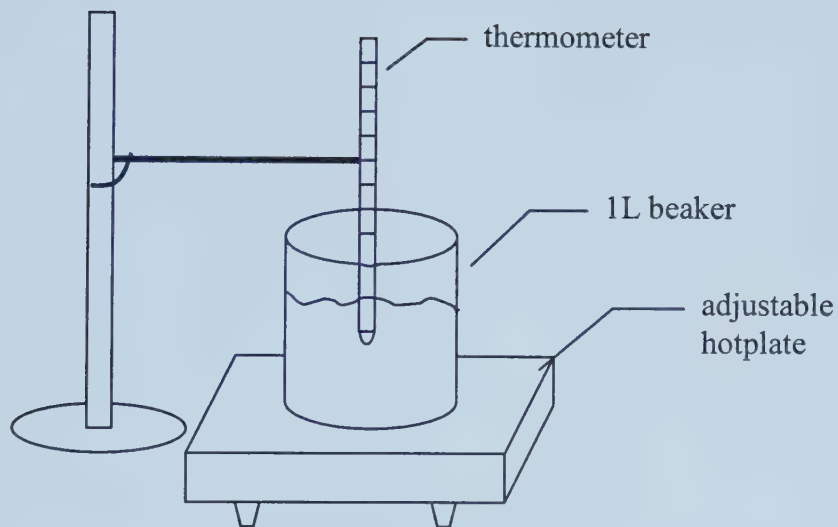
**Table 4.5 Change in *Festuca campestris* plant tiller numbers from pre-treatment, final plant phytomass (at the end of the monitoring period), and accumulated phytomass per tiller, as measured at the end of monitoring 14 weeks following heat treatment.**

Defoliation	Change in tillers · plant <sup>-1</sup>	Final Phytomass (g) · plant <sup>-1</sup>	Accumulated Phytomass (g) · plant <sup>-1</sup>	Accumulated Phytomass (mg) · tiller <sup>-1</sup>
2 weeks	-7 <i>ab</i> <sup>1</sup>	1.44 <i>ab</i>	1.63	55.0
4 weeks	-12 <i>ab</i>	1.20 <i>bc</i>	1.54	40.9
8 weeks	-23 <i>b</i>	0.51 <i>c</i>	1.77	33.3
No defoliation	8 <i>a</i>	2.15 <i>a</i>	2.15	50.9
<i>Standard error</i>	6	0.22	0.25	6.2

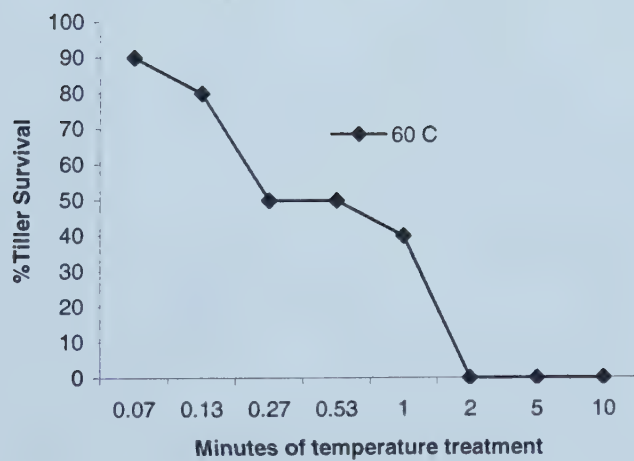
<sup>1</sup> Means within columns followed by different letters differ significantly (p<0.05).







**Figure 4.1** Heated water treatment apparatus for laboratory experiments.



**Figure 4.2** Percent survival of *Festuca campestris* tillers following various exposure times at 60 °C.



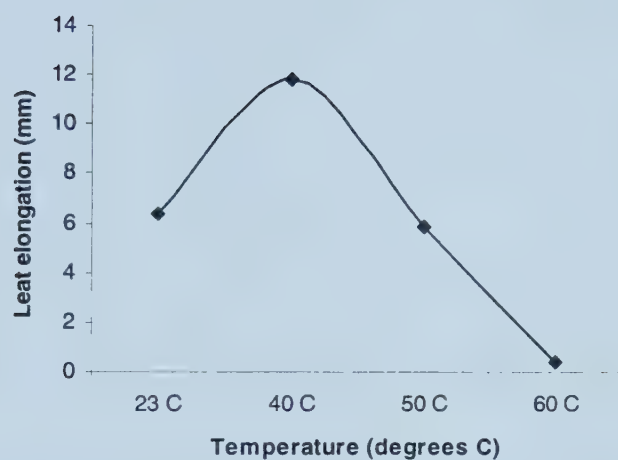


Figure 4.3 Growth of *Festuca campestris* tillers for longer exposure times (1-10 min.) at various temperatures in Experiment 1.

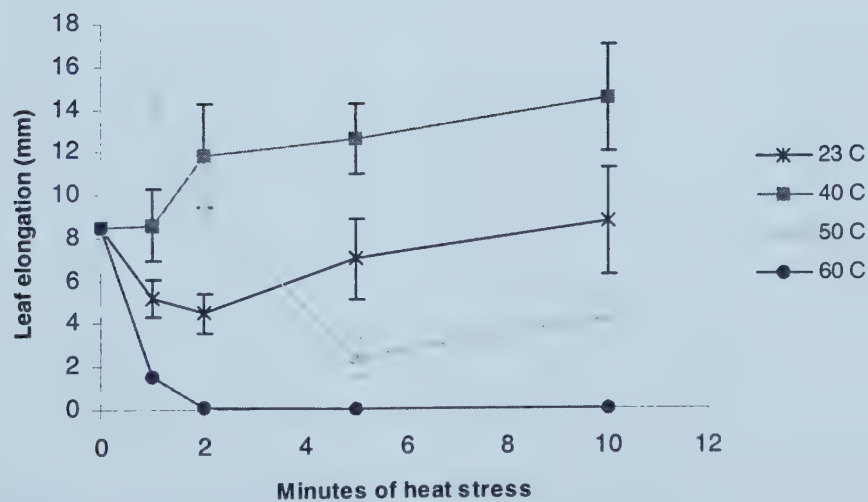


Figure 4.4 Growth of *Festuca campestris* tillers ( $\pm$ S.E.) following exposure to various temperature treatments in Experiment 1.



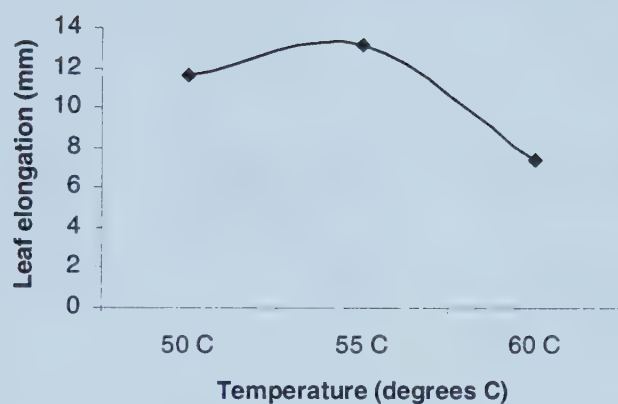


Figure 4.5 Growth of *Festuca campestris* tillers for shorter exposure times (4-32 sec.) at various temperatures in Experiment 1.

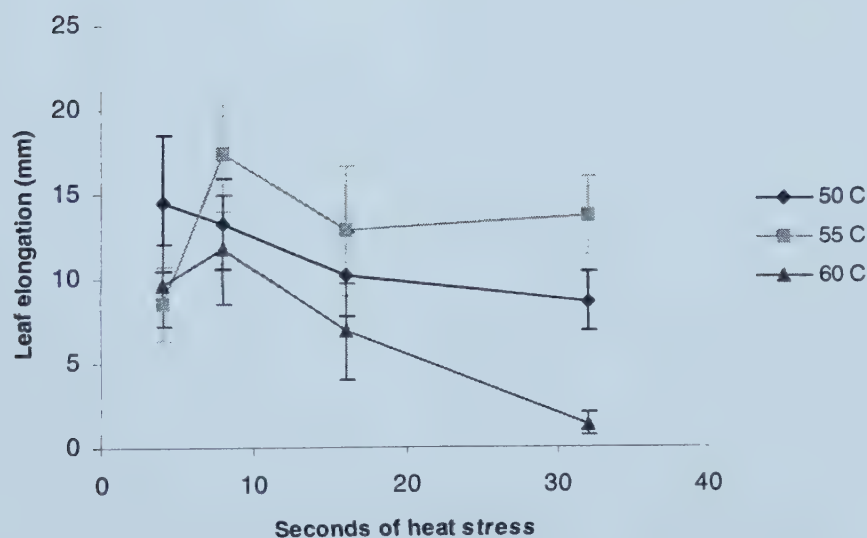


Figure 4.6 Growth of *Festuca campestris* tillers ( $\pm$ S.E.) following exposure to various temperature treatments in Experiment 2.



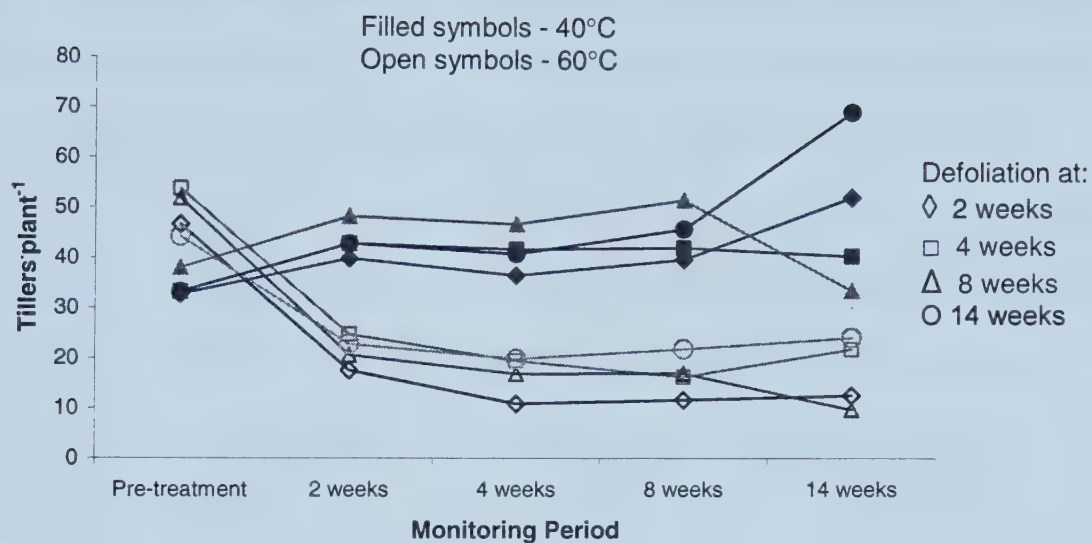


Figure 4.7 Tillers numbers of *Festuca campestris* plants (N=80) subject to 40 or 60°C temperature treatments and defoliated at various times, as measured throughout the 14 week monitoring period. Pre-treatment (heated water bath) tiller numbers are also included.





## 5 Synthesis

As an ecological process, fire was historically important for maintaining plant communities in the Fescue Prairie of southwestern Alberta. Although wildfires still occur in the area (e.g., Bork et al. 2000), a widespread suppression effort for the “protection” of rangeland resources has likely decreased their frequency. Where they do occur, wildfires can decrease forage production and alter rangeland species composition (Antos et al. 1983, Bork et al. 2000). Similarly, with extirpation of free-ranging bison herds, infrequent high density grazing of rough fescue rangeland for short periods rarely occurs under contemporary livestock management systems. The opportunity for cattle to graze selectively under continuous or low intensity rotational systems results in overgrazed patches within which rough fescue can be eliminated (Willms et al. 1985). In contrast, ungrazed patches may also develop, which accumulate litter to the extent that they are avoided by selectively grazing cattle (Willms 1988).

Accumulation of fuel occurs in under-grazed patches and other areas where uneven animal distribution causes areas to remain ungrazed year after year (Willms 1988). This fuel build-up enhances the risk of increased and prolonged elevated temperatures when fire does occur (Morgan 1999), potentially causing greater injury or mortality to plants.

A laboratory experiment was conducted to examine the effects of various exposure times and temperatures on the growth and mortality of rough fescue tillers (Chapter 4). This research demonstrated that greater injury occurs to rough fescue tillers when elevated temperatures are prolonged near growing points, and mortality of tillers can occur if this temperature is sufficiently high. There is also a pronounced interaction



between temperature and exposure time that affects the vigour of rough fescue tillers. A relatively short period of exposure to a high temperature (e.g., >16 sec at 60°C) will cause significant mortality of tillers. However, a longer time of exposure to a lower temperature (e.g., >2 min at 50°C) can have the same effect. In contrast, moderate temperatures may actually stimulate growth of rough fescue tillers. At a temperature of 40°C with exposure times between 1 and 10 minutes, tiller growth was stimulated, as well as at 55°C for short exposure times of 4 to 32 seconds.

An additional laboratory experiment examined the response of individual heat-treated rough fescue plants, and revealed rough fescue plants were tolerant to moderate heat stress. Greater tiller numbers were associated with plants exposed to 40°C for 5 minutes relative to those at 60°C. However, because the study did not utilize a control group, it was impossible to determine if the increased tillering at 40°C was a stimulatory effect. Similar to the heat treatment experiment on individual rough fescue tillers, rough fescue plants were negatively impacted by exposure to 60°C. A reduction in plant tiller numbers and phytomass reinforced the notion that this temperature likely exceeds a crucial threshold for causing injury to rough fescue. Mortality of fescue plants was lower than that of individual tillers exposed to the same time-temperature relationship, probably due to some degree of protection from heat flux provided by the soil and old leaf sheaths surrounding new perennating buds.

The overall sensitivity of rough fescue to high temperatures determined in these studies and the influence that exposure time has on mortality or vigour of rough fescue tillers are important considerations in regard to litter accumulation and distribution on rangeland. Temperatures that plants are exposed to and the duration of that exposure is



correlated primarily to the amount and type of fuel in grasslands (Stinson and Wright 1969, Bailey and Anderson 1980, McDaniel et al. 1997, Archibold et al. 1998, Morgan 1999). The crown meristematic region of bunch grasses is generally protected from fire, as heat does not penetrate very deeply into the soil. However, the amount of fuel above these sensitive areas influences heat flux into soil (Preisler et al. 2000). Consequently, while litter plays an important role in healthy and productive rangelands, too much litter has the potential to be harmful to rough fescue plants when fire eventually occurs. Thus, more research needs to be conducted to determine the level of biomass that causes temperatures great enough or extends exposure time long enough to cause plant mortality or reduced vigour.

As the occurrence of fire increases on rangeland landscapes, whether due to an increase in wildfire or a greater awareness of the benefits of prescribed fire, managers are looking for grazing strategies that will optimize the recovery of rangeland following fire. Rough fescue, given its commercial and practical importance in the Fescue Prairie of southwestern Alberta (Freeze et al. 1999), has inherent value associated with its sustainable use as a forage species. As a result, a field study was conducted at the Agriculture and Agri-Food Canada research substation near Staveland, Alberta, to evaluate the additive impacts of defoliation intensity and times throughout the growing season on foothills rough fescue following an early spring wildfire (Chapter 3).

As might be expected, at the end of the first growing season following fire, burned plants had lower plant and tiller phytomass, and were also shorter than their unburned counterparts. After two growing seasons, however, phytomass and height remained lower for burned plants. Although this finding indicated a reduction in forage





for at least two years, the loss may be partially compensated for by increased palatability due to the removal of standing dead material within the plant or increases in forage quality (Bork et al. 2000, Redmann et al. 1993).

Burning also decreased inflorescence production in the second growing season compared to unburned plants, although unburned plants defoliated in July (near flowering) also had few seedheads. Decreased inflorescence production contrasts with other studies (e.g., Bork et al. 2000) and may have negative implications on areas that have relatively low rough fescue survival following fire and fescue plant propagation through seed is important.

Notably, tiller numbers per plant increased with burning the first growing season following fire. Tiller recruitment was even greater in the second growing season for burned plants, although defoliation during the previous July was able to negate this increase. Increases in tiller number, which reflect increased plant vigour with recovery, suggests that burned plants may have a greater future production potential provided recovery is allowed to occur.

Season of defoliation also showed significant impacts on rough fescue. Although May defoliation was relatively benign compared with other dates based on the response of most variables, a reduction in etiolated growth one year after fire coincided with earlier defoliation and suggested carbohydrate reserves are negatively impacted in the long-term. July defoliation after fire clearly imposed an additive stress on burned plants, reducing long-term (e.g., 2<sup>nd</sup> year) phytomass production and tiller number. Active recovery following fire may coincide with the July period, and defoliation at this time may cause further stress to fescue plants. In contrast, plant growth in May appeared slow



as a result of stress from fire. Thus, plants did not respond as negatively to defoliation due to the relatively small amount of phytomass removal possible at this time compared to plants defoliated in mid season. Unburned plants did not experience any reductions in production or tiller number two years later, suggesting that fescue plants were resilient to one-time defoliation regardless of defoliation date.

Although defoliation intensity (as reflected by stubble heights) had no effect on burned plants two years after fire, more intense defoliation decreased the phytomass and height of unburned plants. Fixed clipping heights used in this study resulted in relatively more phytomass being removed for each defoliation intensity from the taller unburned plants. For burned plants defoliated in May, the difference in clipping heights and slow rate of fescue growth meant that in practical terms, either all the phytomass was removed (high intensity) or none (low intensity).

The fact that the wildfire examined occurred in an area protected from grazing for almost 20 years, and was free of fire for much longer, may have influenced the recovery period of rough fescue plants. Higher temperatures and longer exposure times associated with higher levels of fuel may have caused greater injury to plants. These fire characteristics, combined with lower than normal precipitation (-40%) in the second growing season following fire (2000), may have slowed the recovery of rough fescue plants. Low precipitation in 2000 may also have limited the response of September (e.g., dormant season) defoliated plants compared with those from earlier dates. Defoliated plants would not be able to trap as much snow, which would reduce over-winter soil moisture recharge to the plant. This may be particularly important for plants when moisture is limiting the following growing season, as experienced here.



Changes in plant phytomass and tiller number as a result of a varied defoliation regime were also demonstrated on rough fescue plants brought in from the field, heat treated, and defoliated during regrowth under greenhouse conditions. The greatest decrease in plant tiller numbers and standing crop coincided with deferred defoliation following heat stress. Thus, it appears that fescue plants respond more negatively to defoliation when the latter is timed to coincide with the removal of actively growing vegetation, which in turn has greater impacts on plant recovery mechanisms.

In contrast, early season defoliation in this laboratory experiment seemed once again to have little impact, corroborating the earlier field study. While it is commonly believed that grazing anytime during the growing season is harmful for rough fescue plants, the results found here indicate early season defoliation may not be as negative as previously thought. Alternatively, an early season grazing strategy may be useful for producers unable to secure alternate grazing following fire or those concerned about early growing exotic grasses that are invading native rangeland. Grazing invasive species such as Kentucky bluegrass and smooth brome early in spring may prevent them from expanding vegetatively or setting seed, restoring a competitive edge to native species. This suggestion assumes, however, that rough fescue will not be preferentially selected over introduced soft grasses and that the latter are indeed available for grazing within the burned area. Tame forage species are generally more palatable early in the growing season, but changes in herbage quality, and therefore palatability, of native species following fire may influence grazing preference. More research needs to be conducted to determine cattle grazing preferences following fire on native rangeland with complex mixtures of species.



Managers can mitigate potential negative impacts of fire on rough fescue before fire occurs by manipulating fuel loads through improved animal distribution or more frequent prescribed fire. In the event that fire does occur, a land manager's best option is likely to defer grazing at least one growing season. Spring grazing burned areas may be possible without increasing damage to rough fescue as defoliation at this time produced a similar long-term above-ground plant response as dormant season defoliation. This conclusion is based on the assumption that alternative forage (e.g., introduced soft grasses) will be available. However, carbohydrate reserves may be more negatively impacted and may affect longer-term plant survival. Most importantly, grazing in July should be avoided on burned and unburned areas as it reduces short and long-term rough fescue phytomass and vigour.



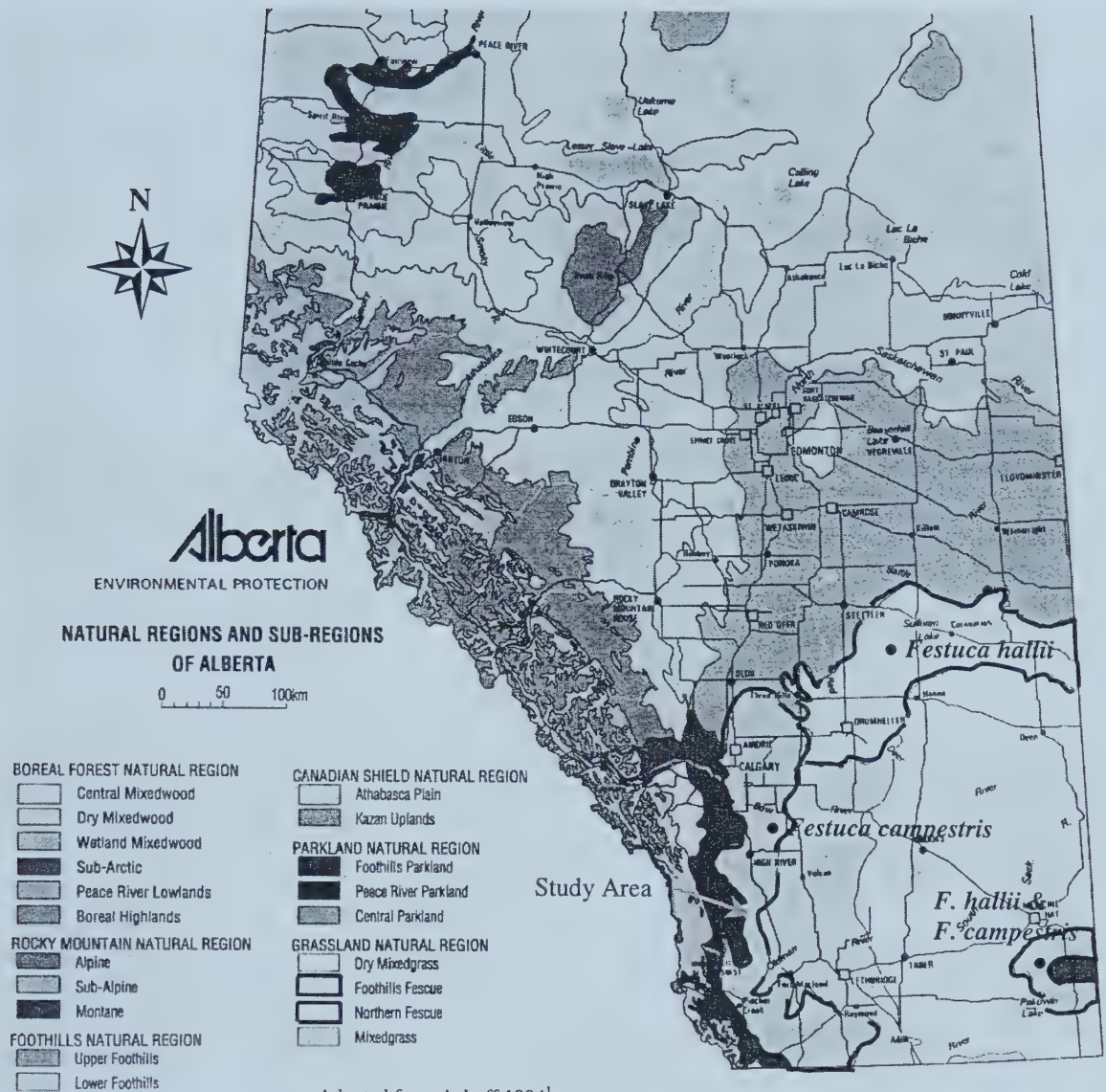


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## Appendix 1



Adapted from Achuff 1994<sup>1</sup>

Produced by Alberta Parks Services, Management Support Division.

<sup>1</sup> Achuff, Peter L. 1994. Natural regions, subregions and natural history themes of Alberta. Natural Regions Report No. 3. Alberta Environmental Protection, Edmonton.

















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